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Proceedings— Conifer Tree Seed in the Inland Mountain West Symposium

Missoula, Montana, August 5-6, 1985

FOREWORD

The symposium "Conifer Tree Seed in the Inland Mountain West" started, developed, and matured in much the same manner and time frame as many conifer cone crops. Like the biological stresses that often stimulate cone production, the stress of knowledge needs prompted the initiation of this symposium.

The first suggestion that a symposium be held to consolidate the available cone and seed knowledge came at a January 27, 1983, meeting of Forest Service Intermountain Station and Northern Region scientists discussing cone and seed production information needed to enhance natural and artificial regeneration in the Northern Rockies. Like the initiation of a cone bud, the idea for a symposium was nothing really new, it just came at the right time and fell into a fertile environment of silviculturists, geneticists, and entomologists.

A steering committee, chaired by Dr. Raymond C. Shearer of the Intermountain Research Station, was formed and proceeded with the planning. Committee members were: Dr. George Blake, School of Forestry, University of Montana; Mr. Jerald E. Dewey, Pest Management, Northern Region, Forest Service; Dr. A. K. Hellum, Department of Forest Science, University of Alberta; Dr. George E. Howe, Division of Timber Management, Northern Region, Forest Service; and Mr. Wayne Maahs, Forestry Division, Champion International Corporation. The School of Forestry and Center for Continuing Education of the University of Montana handled many of the logistical details for the symposium and the Intermountain Research Station edited and published the proceedings.

Numerous meetings, letters, announcements, coordination sessions with authors, and a host of other details preceded the very successful symposium, August 5-6, 1985. Included were 40 papers presented by silviculturists, geneticists, entomologists, physiologists, pathologists, nurserymen, and others. The objective of the symposium--to consolidate information and research conducted on conifer tree cones and seeds native to the Inland Mountain West of the United States and Canada--was met, and 164 attendees left with a much better idea of what is known about western conifers. This symposium culminated efforts of many people, and, like a cone that survives all the hazards and produces seed at the end of its development period, succeeded in producing a very viable proceedings.

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CONTENTS

SEED CONSERVATION PROBLEMS: NATURAL AND UNNATURAL

J. Derek Bewley and Andrew D. Powell

ABSTRACT: The majority of seeds respond to storage conditions in an "orthodox" manner, in that a low seed moisture content and low temperature prolong their storage life. Deterioration can take place in the seemingly "dry" stored seeds, perhaps largely due to physico-chemical processes. The consequences of deterioration to metabolic integrity of the seeds are various, but macromolecular damage, leading to defective membranes and damaged organelles are manifestations. Storage of seeds in the imbibed state, a condition in which many seeds find themselves in "natural" storage conditions in seed-soil banks, may prolong their longevity. Hydration may allow the seeds to put into operation the repair mechanisms essential for the maintenance of their metabolic integrity. The cost, however, is the consumption of reserves to provide energy, which may eventually become depleted. Recalcitrant seeds cannot withstand drying and must be stored in a wet state. These latter seeds might persist better as seedlings, and the preservation of difficult seed species (both orthodox and recalcitrant) in seedling banks is a possible strategy.

INTRODUCTION

The seed is the dispersal stage of the plant life cycle and, in many instances, it is the only stage which can survive severely adverse environmental conditions. A low water content (usually some 5-15%), combined with an inherent ability of the cells to withstand severe water loss, facilitate the seed's survival. In the dry state, many seeds can withstand extremes of cold (storage in liquid nitrogen is becoming an increasingly common practice for genetic stocks of seeds) and heat (on the desert floors temperatures may exceed 75°C). As a general rule, commercial storage of seeds takes advantage of their ability to retain metabolic quiescence in the dry state, although other factors must be considered, as will be discussed later.

Seeds which retain their viability in the dry state, and can be stored thus, are regarded as conforming to the general "rules" for storage conditions; such seeds are described as showing orthodox viability characteristics. The seeds of all common agricultural and horticultural crop species which are annual or biennial exhibit this orthodox storage behaviour. There is another group of species, however, which produce seeds that normally never dry out on the mother plant, which are dispersed in the moist condition, and which are killed if their moisture content declines below some relatively high critical value. Since these seeds do not conform to the rules of storage that are applicable to the orthodox ones, such desiccation-tolerant seeds have been designed as recalcitrant (Roberts 1973).

In this paper we will consider some of the problems associated with the storage of orthodox seeds in the dry state--a common practice, but an unnatural condition for many seeds to find themselves in for protracted periods. More naturally, when many seeds are shed from the mother plant they remain buried in the substrate, often in an intermittently wet state. Such seeds can withstand drying, however, which is in contrast to the situation in recalcitrant seeds, for these must be kept constantly in a near-hydrated state.

ORTHODOX SEEDS AND DRY STORAGE

Premature Drying of Seeds for Storage

Acquisition of desiccation-tolerance during seed development occurs approximately at the midway stage, e.g. in *Ricinus communis* (Kermode and Bewley 1985a), *Pisum sativum* (Rogerson and Matthews 1977), and *Glycine max* (Adams and others 1983). Prior to this time, premature desiccation generally results in poor recovery of germinability of the seed upon subsequent rehydration. There is a concomitant reduction in the metabolic capacity of the seed, e.g. for protein synthesis, when one attempts to germinate seeds following drying during this desiccation-intolerant stage (Dasgupta and others 1982). Immature seeds exhibit a great variation in the rate of water loss that they can tolerate. Thus, when we refer to a developing seed acquiring desiccation-tolerance, we must define also the rate of water loss tolerated. For example, *Phaseolus vulgaris* seeds can tolerate extreme rates of drying, i.e. rapid desiccation over activated silica gel (Dasgupta and others 1982), from about the 26th day of development (of a 42-day developmental cycle), whereas in *R. communis* tolerance of such extreme rates

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of water loss is not acquired until the 55th day of a 60-day developmental cycle (Kermode and Bewley 1985a). On the other hand, this latter seed can withstand slow water loss, even to complete desiccation, at a stage less than half-way through its development, and can germinate fully upon subsequent rehydration. Seeds of Glycine max also require slow dehydration (which can be achieved while they are in the pod) to survive premature drying; those shelled before drying lose their viability (Fjerstad and others 1981; Adams and others 1983). The advantage of the slow water loss is that it may permit membranous structures within cells to undergo certain reversible conformational changes during desiccation, thus allowing them to retain their integrity (Bewley 1979; Fjerstad and others 1981). Thus, upon rehydration, metabolism within reasonably intact cells can recommence, and the appropriate germination mechanisms can be put rapidly into effect. Rapid drying of immature seeds, on the other hand, may lead to irreversible cellular changes which are too extensive for repair to be effected in the germinating seed, with a consequent decline in, or loss of, viability.

Premature harvesting of seeds while in the desiccation-tolerant stage of development might be advantageous, in some instances, for the subsequent establishment and growth of the progeny. Studies on the endosperms of developing seeds of R. communis (Kermode and Bewley 1985b) show, for example, that synthesis of certain protein fractions (including the soluble and major insoluble storage proteins) reaches a peak at about the midway point of development (fig. 1A). Later in development protein synthetic activity declines; after 45-50 days of development this decline is because the seed is drying out as it reaches the latter stages of maturation. Hence the seed's synthetic potential changes with time during development. When the seed is dried prematurely at 30 days of development it survives, and upon rehydration its rate of synthetic activity is considerably higher than in germinating mature dry seeds or in 40-day dried and rehydrated seeds (fig. 1B). Hence there is a strong correlation between the competence of the seed to conduct protein synthesis prior to premature drying and its competence to carry out this synthesis upon subsequent rehydration--even though the products of protein synthesis formed during development and germination are very different (Kermode and Bewley 1985b; Kermode and others 1985). If the high synthetic capacity also has a bearing on the survivability and germinability of seeds (i.e. if there is increased viability because of an increased potential for synthetic activity) then it might be of value to harvest certain species of seeds prematurely, during the desiccation-tolerant stage, when the capacity for cellular activity of the seeds is highest. Following the appropriate drying regimes, and under suitable storage conditions, the chances of maintaining seed viability might be greater.

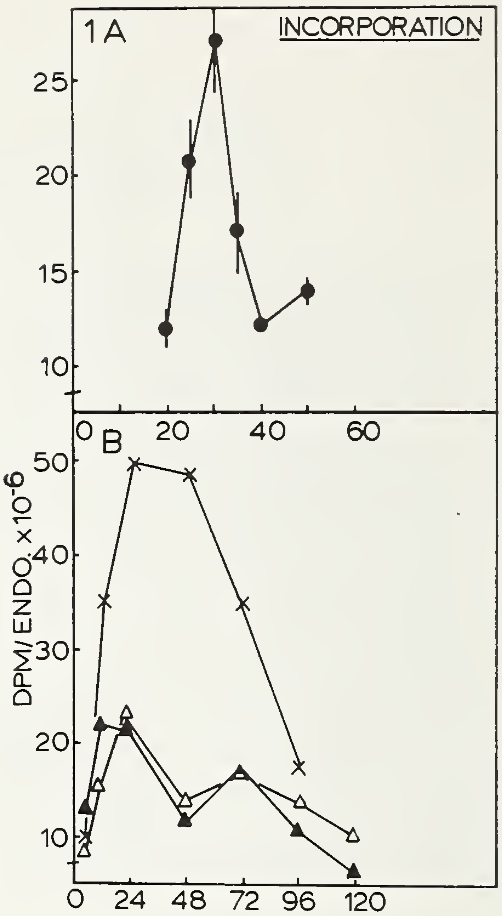

Figure 1.--Incorporation of ^{3}H-leucine into (A) developing seeds of Ricinus communis harvested at 20-50 days after pollination (DAP) and (B) following mature seed imbibition 5-120 hours after imbibition (HAI) (▲); following rehydration of desiccated 40 DAP seeds, 5-120 HAI (△); and following rehydration of desiccated 30 DAP seeds, 5-120 HAI (X). Note that the high synthetic activity of 30 DAP seeds is maintained upon rehydration following premature desiccation. After Kermode and Bewley (1985b).

Some studies have been carried out to determine if the maturity and quality of tree seeds at the time of collection have an effect upon subsequent germinability. The general consensus appears to be that early harvesting is not necessarily advantageous and, indeed, in some instances it may be disadvantageous (Wang and others 1982). In no case, however, were correlations made with metabolic activity during development, nor was storeability of the seeds a factor under consideration.

Viability of Seeds in Dry Storage: Optimizing Conditions

The majority of seed species are of the orthodox kind in relation to storage and conform to certain general rules that predict the pattern of loss of viability in relation to their storage environment (Harrington 1973).

Rule 1 states that for each 1% decrease in seed moisture content the storage life of the seed is doubled;

Rule 2 states that for each 10°F (5.6°C) decrease in seed storage temperature the storage life of the seed is doubled;

And Rule 3 combines these observations to state that the sum of the storage temperature in degrees F and percent relative humidity (RH) must not exceed 100, with no more than 50% of the sum being contributed by the temperature.

At high seed moisture contents (>30%) non-dormant seeds will germinate, and from 18-30% moisture content rapid deterioration by microorganisms may occur, particularly in the presence of oxygen. Fungi will grow on seeds at 10-18% moisture content, and above 18% the stored seeds may respire and deplete essential reserves. An additional problem arises under conditions of poor aeration, for both seed and fungal respiration could generate enough heat to kill the seeds. Below about 10% moisture content insect activity is diminished, and at 5-7% moisture content the seeds are metabolically quiescent. A low moisture content of 4-5% seems to be less desirable for long-term storage than one of 6-7%, for reasons which are not abundantly clear.

The use of cold temperatures in storage has a generally beneficial effect on longevity. At liquid nitrogen temperatures seeds may survive indefinitely (Stanwood and Bass 1981). Longevity at -20°C for many seeds is considerably prolonged --the required regeneration interval for Pisum sativum stored at -20°C and 5% moisture content may exceed 1000 years, for example (Roberts and Ellis 1977). Even storage at 0-5°C will improve the longevity of seeds, as would be predicted by Rule 2, provided that certain precautions are taken--particularly ensuring that the stored seeds do not pick up moisture resulting from increased atmospheric humidity at low temperatures.

The extension of the interval between successive regenerations of seed stocks in storage has been a major aim. This not only eliminates the need to devote time (and money) into seed stock regeneration but also eliminates the rate of genetic drift which might take place in the small seed batches planted out from the stored stocks. Repeated regenerations can also put the seed stock at risk of diseases and other environmental stresses which might prove to be fatal.

While considerable attention has been paid to results from germination tests, more recently there has come the appreciation that seed batches with the same germinability can perform differently in the field, i.e. seed batches with similar viabilities have different vigour levels. The International Seed Testing Association has defined seed vigour as "the sum total of those properties of the seed which determine the potential level of activity and performance of the seed or seed lot during germination and seedling emergence" (Perry 1978). Vigour tests have been developed (Perry 1981) which when used in conjunction with the standard germination test allow the identification of a seed batch which might not establish a good stand after germination even though germination test values were the same. These tests identify the fact that deterioration in the performance of a seed can take place in storage even though high germination levels are maintained. As we shall see later, some metabolic lesions may contribute to a loss in vigour as well as viability, but handling of the seeds prior to harvest is also important. The long-term storage of a seed lot with an initial low vigour is a waste of precious resources.

The drying of mature seeds for storage can be problemmatical, particularly in cases where complete loss of water has not occurred on the mother plant. In the previous section we outlined how drying of prematurely harvested seeds may have to be carefully controlled. Such is also the case for some seeds harvested at 15-20% moisture content and then dried to some 5-7% moisture content for storage. Elevated temperatures during drying or drying too quickly or excessively can reduce viability and vigour, although under good management this should not occur (Rampton and Lee 1969). Care must also be taken during mechanical harvesting and processing to reduce the damage to the outer seed structures since this might lead to damage when imbibition takes place. The moisture content of seeds will play an important role in their ability to withstand harsh mechanical handling (Powell, A.A. and others 1984).

The viabilities expressed by populations of mature dry seeds before and during storage are very variable; for many agricultural and horticultural species it is usually, and acceptably, very high --in the range of 95-98%. Viabilities of other species, including forest species, are frequently much lower. In some instances relationships are to be found between mature seed characteristics and viability. In several Pinus spp., for example, there may be a correlation between mature seed weight and germination percentage, and also correlations with seedling vigour (Ghosh and others 1976; Kandya 1978), although this may not always be the case (Chauhan and Raina 1980). From a practical point of view, sorting of seeds by weight before planting may not be desirable, and it may be best to use all viable seeds for reforestation (Hellum 1976). The weight of white spruce seeds seems to be highly specific for an individual tree and thus there might be a reduction in genetic variability if seeds are sorted by weight.

Metabolic Changes Occurring During Seed Storage

We may wonder how a dry seed, in a state of metabolic torpor, can undergo deterioration in storage--and how this can be prevented. Under conditions where the cells of the seed are partially hydrated in storage a limited amount of metabolism might take place, which could be detrimental. Partial completion of anabolic or

catabolic pathways could lead to the accumulation of undesirable metabolites, resulting in a potentially fatal disequilibrium, which cannot be rectified upon subsequent reimbibition.

The metabolic manifestations of deterioration in dry storage are many, and have been detailed in several reviews (Bewley and Black 1982; Osborne 1980; Roberts 1975, 1981). A summary of the various metabolic lesions that occur during storage and which result in a loss of viability is presented in fig. 2. Any single lesion could result in a complete loss of germinability or simply a reduction in vigour, depending upon its quantitative expression within the cell. It is more likely, however, that aging elicits a number of distinct lesions (perhaps none of them fatal by themselves) which together reduce the seed's ability to survive.

Of the cellular changes which take place in the dry state, those to membranes have attracted the most interest. This is because the integrity of the plasmalemma and associated membranes (endoplasmic reticulum) is an integral requirement for normal cellular function, and efficient mitochondria are required for the maintenance of a favourable energy status. A loss of integrity of the plasmalemma and tonoplast in aged seeds is implied from observations that more substances leak into the imbibition medium from such seeds than from unaged ones (Ching and Schoolcraft 1968; Parrish and Leopold 1978). Excess leakage from deteriorated seeds may represent a loss of respirable substrate, but quantitative correlations between this loss and subsequent germinability have not been made. In some instances, increased leakage of organic metabolites might lead to a secondary damaging effect by stimulating growth of contaminating microorganisms on the seed surface.

The cause of the changes in membrane integrity during seed aging in storage has not been elucidated, and there is little agreement between workers on the deteriorative changes suffered by phospholipids, the major membrane component. In some seeds there is reasonable evidence that a decline in unsaturated fatty acids, e.g. linoleic and/or linolenic acids, can be correlated with loss of germinability, e.g. in slowly aged *Glycine max* (Priestley and Leopold 1983) and *Trifolium subterraneum* (Flood and Sinclair 1981). Seeds of *Acer platanoides* when subjected to an accelerated aging treatment (i.e. by being placed in a saturated atmosphere at 30°C) exhibit a marked decline in germination, which is accompanied by a loss of phosphatidyl choline and phosphatidyl glycerol from the membrane fraction (Pukacka 1983). The cause of the changes in fatty acid characteristics of dry seeds, and hence their loss of viability, has been attributed to physico-chemical perturbations of these molecular components of the membranes. In particular, peroxidation has been singled out as a major causative agent, with the auto-catalytic oxidation of unsaturated fatty acids (e.g. linoleic acid and linolenic acid) by atmospheric oxygen in a free-radical chain reaction occurring in the dry seed. However, the evidence for lipid peroxidation in aging seeds is tenuous, and that which is in its favour is largely circumstantial (Harman and Mattick 1976; Koostra and Harrington 1969).

There are enzyme (e.g. superoxide dismutase) and scavenger systems present within seeds which can reduce the activity of free radicals. Correlations between endogenous superoxide dismutase activity and viability of seeds have been attempted, but no definitive role can be assigned to this enzyme as far as the restriction of peroxidation is concerned (e.g. Stewart and Bewley 1980). Tocopherols are organic free radical scavengers and it is estimated that one molecule of this compound can afford antioxidant protection to several thousand fatty acid molecules. Attempts to correlate tocopherol levels with susceptibility to peroxidation damage have been without success; in aged soybean seeds, for example, tocopherol levels are the same as in

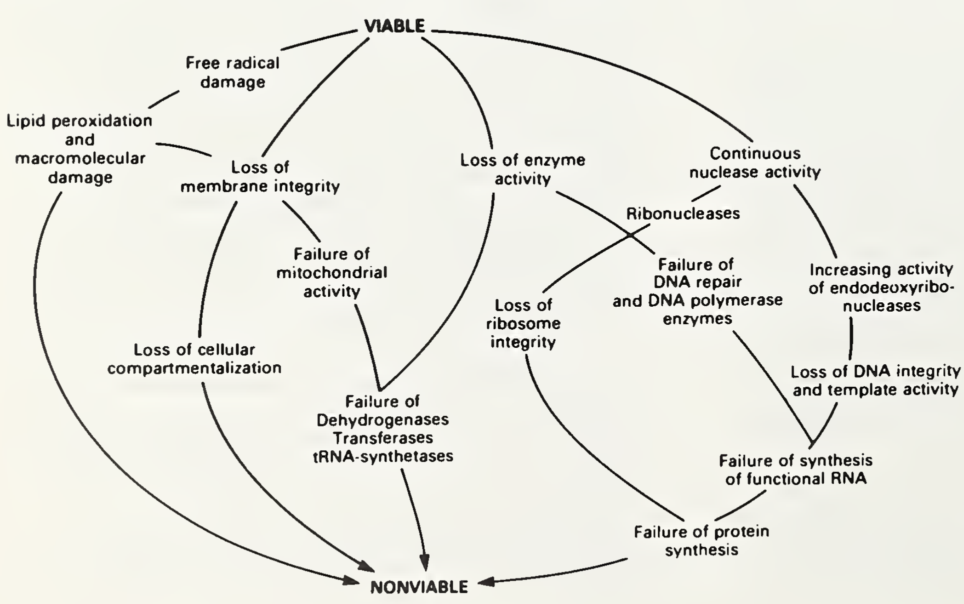

Figure 2.--A scheme to explain the potential causes for loss of viability in stored seeds. Adapted from Osborne (1980).

unaged controls (Priestley and others 1980; Fielding and Goldsworthy 1980). On the other hand, it appears to be beneficial to add anti-oxidants to isolated membrane preparations, or to seeds (Fielding and Goldsworthy 1980; Basu and Dasgupta 1978).

Some restorative treatments have been attempted to increase germinability of seeds subjected to loss of viability in dry storage. Hydration of seeds in atmospheres of high relative humidity before being placed in water is beneficial to unaged seeds (Simon and Raja Harun 1972; Powell and Matthews 1978), and may be of value in encouraging germination of aged ones. Improved germinability or growth of seeds with reduced viability or vigor can be achieved, for example, by subjecting them to conditions that permit low, or slow, water uptake, e.g. by "flash imbibition" of wheat (Goldsworthy and others 1982); by placing seeds in an atmosphere of high relative humidity (Basu and Pal 1980; Sanchez and Miguel 1983); or by imbibing seeds initially in an osmoticum, such as polyethylene glycol (Brocklehurst and Dearman 1983; Burgass and Powell 1984). Presumably the initial slow hydration of the seeds allows for the ordered rearrangement or repair of membranes before the inrush of water associated with imbibition from the dry state, which might otherwise be too sudden and disruptive.

Whatever the real causes of deterioration in dry storage are, it is evident that they take place while the seed is in a state of quiescence or near-quiescence, and while it has little chance to accommodate the changes which are taking place within its cells. Only inherent defense mechanisms, such as those against free-radical damage, can be brought to bear. It is unlikely that seeds can be treated in advance of storage to prevent deterioration, although storage conditions can be devised which minimize damage (e.g. low temperatures and a dry atmosphere). But as we will consider now, maintenance for long periods in the dry state is not the natural way for many seeds to be stored. Rather, as they lie in the ground, they are intermittently to frequently wetted, and hence undergo periods of both metabolic activity and relative quiescence.

SEEDS IN THE SOIL: THE NATURAL SEED BANK

The Soil Seed Bank

Seeds buried in the soil for long periods must be able to cope with a series of problems, not least of which are the necessity to sustain themselves metabolically when hydrated and to remain in a dormant state until appropriate germination and growth conditions are available.

There is an appreciable reserve of viable seeds in the soil underlying a wide range of plant communities. The species composition of a seed bank reflects the differing strategies of past and present components of the vegetation, and a great diversity is often apparent (Roberts 1981). Studies of the litter and surface soil layers of North American forests have shown the presence of viable seeds of species not represented in the vegetation, thus indicating long-term survival of species even from previous successional stages (Livingston and Allessio 1968). An indication of the seed banks present in some western forest stands is presented in table 1. In coniferous forests there is a virtual absence of viable seeds of the dominant tree species, owing to low seed inputs and rapid losses from the surface seed bank (Kellman 1974; Whipple 1978). The predominant seeds present are those which arise after clear-felling. In the U.S.S.R. the number of viable seeds present in the soil of a 100-year-old southern tiaga forest (*Picea abies* and *Vaccinium myrtillus*) was in the order of 1200-5000 m^{-2} (Karpov 1960). But little correspondence was found between the floristic composition of the ground flora and that of the seed bank, the latter being comprised of species involved in early successional stages, or present in clearings. In old and comparatively undisturbed *Picea* or *Picea*/*Pinus* forests in the Moscow area (Petrov 1977) species of seeds of herbs and shrubs were present even though the vegetative stages of these species were virtually absent from the vegetation.

Table 1.--Some examples of viable seeds present in the soils of Western North American forests

Province or state	Major forest species	Age of stand (years)	Depth of burial (cm)	Seeds per m^2
British Columbia	*Tsuga heterophylla* *Pseudotsuga menziesii*	100	0-10	1016
Oregon	*Abies grandis* *Pinus contorta*	130	litter + 4	421
	Abies grandis *Picea engelmannii*	150	litter + 4	1863
	Abies grandis *Larix occidentalis*	175	litter + 4	3447
Colorado	*Picea engelmannii* *Abies lasiocarpa*	325	0-5	53

Excerpted from Roberts (1981)

In northern hardwood stands the situation is somewhat different. Analysis in the spring of such stands in Pennsylvania dominated by Prunus serotina, Acer saccharum or Acer rubrum showed that they contain seeds of P. serotina, P. pensylvanica and Betula spp. in the soil (Marquis 1975)--about 370 m^{-2}. Seeds of some species (A. saccharum, Tsuga canadensis and Fagus grandiflora) germinated mainly in the first spring, and hence were only transiently present in the seed soil bank. Other species survived for up to 5 years (Fraxinus americana, P. serotina and Betula spp.), while high numbers of P. pensylvanica seeds remained viable in the soil for in excess of 30 years after this species had died out of the overstory. Evidence for even more persistent seeds in a forest understory has been presented: seeds of Comptonia peregrina have survived for 70 years or more beneath a Pinus strobus forest in Connecticut (Del Tredici 1977).

In general, though, most of the shade-tolerant true forest species do not produce seeds which enter the buried seed bank. This is also generally true for the dominant trees of mature forests. The greatest number of seeds present in the soil beneath closed forest or woodland are those of species commonly found in more open habitats such as clearings or the early stages of secondary successions. Such seeds may persist in the soil for 30 years or more.

Contrasting this situation in forest soils is that which exists in arable and grassland soils. In arable soils the average number of viable seeds at plough depth (to approx. 20 cm) usually exceeds 4000 m^{-2}, and in very weedy fields may be around 75000 m^{-2} (Jensen 1969). The main contributors to banks of arable seeds are the annual weeds, which often account for at least 95% of all seeds; those of perennial weeds and crop species are only poorly represented. Quite often there are one or two species which have seed numbers much greater than the rest.

Seed Burial and Dormancy

The probability that a seed will remain viable in the buried state is enhanced by the presence of dormancy mechanisms which delay germination in the period immediately following seedfall. Some seeds are dormant when they are shed from the mother plant, and are said to exhibit an innate or primary dormancy (Harper 1957; Bewley and Black 1982). Others acquire dormancy after shedding and are said to exhibit enforced dormancy or secondary dormancy (Harper 1957; Bewley and Black 1982). Some examples of primary dormancy are characteristic of the embryo, and include the need for an extended period of incubation in warm moist conditions to allow maturation of the embryo, inhibition of germination by light or a specific requirement for stimulation by light, or a requirement for chilling. Another type of dormancy mechanism is coat-imposed, due to some sort of mechanical restraint set up by the structures surrounding the embryo. The secondary dormancy which develops in already dispersed, mature seeds is enforced when seeds are prevented from germinating by the unfavourable conditions prevailing in the habitat in which they find themselves.

Germination of buried seeds may be held in check for many years, often until some disturbance occurs. If cultivated soil is turned over, or if a natural disturbance takes place as in a river bank, many of the buried seeds germinate and a flush of seedlings results. A major factor in the promotion of germination is light, and as little time as half a second exposure to full sunlight can cause many seeds to germinate and produce seedlings (Wesson and Wareing 1969a,b; Sauer and Struik 1964). It has been reasonably concluded, therefore, that many seeds which are light-requiring normally fail to germinate because burial in soil excludes the light. But many of the species that appear after soil disturbance are known to produce seed which, when freshly shed from the mother plant, are capable of germinating in darkness. Hence seeds of such species must acquire a light-requirement when buried (Wesson and Wareing 1968; Taylorson 1972). This is because burial induces a secondary dormancy by mechanisms which still remain to be explained. Light sensitivity may also be lost during burial, e.g. as in Barbarea vulgaris, the seeds of which are light sensitive when freshly dispersed, become insensitive to light after a period of burial, and then acquire light sensitivity once more (Taylorson 1972).

The effects of light in relation to burial might act to secure the most favourable position in the soil for germination. It would be undesirable for small seeds to commence germination at too great a depth in the soil since, because of their limited food reserves, they may be unable to grow sufficiently to reach the light and become autotrophic.

Besides absolute exposure to light, exposure to light of appropriate wavelengths is also important for germination. The spectral energy distribution of sunlight passing through a canopy of leaves is greatly reduced in the dormancy-breaking red region, and is relatively enriched in the far-red region (Holmes and McCartney 1975). Some seeds, therefore, will become dormant as a result of irradiation with canopy light and will germinate only later when a dormancy-releasing factor, such as chilling or light (usually direct sunlight) has been experienced (Fenner 1980). This mechanism explains the paucity of seedlings on forest floors and the flush that follows clearing in the leaf canopy, brought about when individual trees die and fall, or when tree removal occurs.

The second major environmental factor which promotes the germination of seeds in the soil bank is temperature. Seeds whose dormancy is broken by chilling will germinate when temperatures begin to rise in early spring, which has dual advantages. Firstly, the emergence of seedlings is prevented immediately before inhospitable winter conditions; secondly, seedlings can establish themselves prior to extensive shading by leaves. Hence species

inhabiting deciduous woodlands, including the nascent tree seedlings themselves, derive benefit by germinating before the leaf canopy appears. Germination of buried seeds in situ is often brought about by a response to diurnal fluctuations in temperature which may result from the removal of the insulating layers, such as canopy foliage, litter or humus (Grime 1979). Different sizes of gaps in the overlying cover influence the amplitude of the temperature fluctuation, which in turn appears to correlate with the germination percentages. The capacity to respond to particular amplitudes of temperature fluctuation in darkness may act as a depth-sensing mechanism, such that the dampening of the amplitude can be used by dormant seeds to determine the depth at which they are buried. Clearance of vegetation can therefore have important effects in addition to an alteration of the light environment in the top layer of the soil; thus buried seeds can use both temperature sensitivity and their phytochrome system to give them positional information (Thompson and Grime 1978).

Seeds of any species represented within a seed soil bank exhibit polymorphism with respect to their germination requirements. Seeds produced by the same population of plants (Grousiz and others 1976) or even by one individual plant (Cavers and Harper 1966) may show considerable differences in their response to environmental cues, and there may be very wide variation with respect to the amplitude of diurnal fluctuation in temperature required to initiate germination. This is of great value in environments where the risks of seedling mortality are high and synchronous germination of the seed bank could put the population in peril of extinction.

Although seeds in soil banks display polymorphism in their germination requirements, which is of considerable importance for the maintenance of their genetic diversity and for recolonization, the recurrent germination of seeds from the soil seed bank is a financially draining problem for farmers, who must combat persistent weeds like wild oats, wild mustard and redroot pigweed. Efforts have been made to "flush" the soil with promoters to induce the stored population to germinate simultaneously. Success has been very limited, although application of ethylene to the soil does break the dormancy of some buried species (Schonbeck and Egley 1981).

Seedling Banks - A Form of Persistence for Forest Species?

For many forest species the time between seed shedding and germination is relatively short (van der Pijl 1972), although among temperate forest trees it is not uncommon for germination itself (e.g. Fagus sylvatica) or plumule extension (e.g. Quercus petraea) to be temporarily delayed. Such seeds do not accumulate in persistent seed banks, however. In mature temperate forests a common regenerative strategy is for tree seedlings and saplings to persist for long periods in a stunted or etiolated condition (table 2). A small percentage survive to maturity by expanding into canopy gaps resulting from natural or man-made clearings. Many forest trees do not produce seeds each year, and the ability of seedlings to survive unfavourable conditions for long periods ensures that the potential for regeneration is maintained. One factor which may contribute to survival in the seedling state is the size of the seeds of temperate forest species (Ng 1978). They are often large in relation to seedling growth and may provide an effective nutrient source during the initial establishment in heavily shaded and/or nutrient-deficient environments (Grime and Jeffrey 1965).

Table 2.--Forest species which can regenerate by means of persistent seedlings

Species	Location of study
Hemlock (Tsuga canadensis)	N. America
Norway spruce (Picea abies)	Sweden
White oak (Quercus alba)	N. America
Holly (Ilex aquifolium)	U.K.
Sugar maple (Acer saccharum)	N. America
Beech (Fagus grandiflora)	N. America

After Grime (1979)

STORAGE IN THE IMBIBED STATE

Almost any combination of time, temperature and moisture content will result in loss of viability of dry stored seeds and will result in some genetic damage in the survivors. Increasing chromosome damage occurs with increased periods of storage, and this is manifested in an increased number of aberrant cells (Roberts 1975). While accumulation of genetic damage in stored seed lots that are planted for food or feed production may be of little consequence, unless expressed in the first generation of planting, such damage in seeds grown for germplasm stock may have more serious long-term implications. A stored seed lot with little reduction in viability could harbour a considerable number of mutations, which would not be expressed immediately in the generation grown from that seed, but which would begin to segregate in subsequent generations, and in all those thereafter.

Why aging seeds accumulate chromosome damage is not understood, but it is apparent that it can be circumvented if seeds are stored in the imbibed state. When seeds of lettuce (Lactuca sativa) and ash (Fraxinus excelsior) are maintained in a fully imbibed state, in a dormant condition, they maintain their full capacity for germination for years, and yet sustain very little chromosome damage (table 3). Loss of viability from seeds stored at low moisture content (approx. 10%) might result from inactivity of enzyme systems capable of repairing storage-induced damage to DNA, and also to other essential macromolecules (and organelles in the cytoplasm). Assuming that repair can only occur successfully in the fully imbibed state, then any damage suffered by

the wet-stored seeds will be continuously repaired and will not accumulate. In dry-stored seeds, the repair mechanisms will become activated upon imbibition after storage, but by this time the damage might be so extensive and beyond restitution that viability would be lost.

Table 3.--Effects of a six-month storage period at different water contents on the germinability and extent of chromosome damage in radicle tips of germinated lettuce seeds

% Moisture content of stored seed	% Germination	Aberrant nuclear divisions
9.7	17	45
7.0	80	17
5.1	100	10
100	100	2
Not stored	100	2

After Villiers (1974)

While storage of seeds in an imbibed state (or even intermittently imbibed) may be of advantage, it is pertinent to ask: how do such seeds maintain themselves metabolically without exhausting their energy sources? Recent work on imbibed-stored lettuce seeds (Powell, A. D. and others 1983, 1984) shows that when these are maintained in darkness at supra-optimal temperatures (25°C) they enter a condition of secondary (skoto-dormancy) dormancy from which they cannot be aroused by conventional dormancy breaking treatments (e.g. red light or gibberellic acid). This loss of response occurs over a 1-3 week period. Initially, as the seeds remain in the primary dormant condition there is an increase in oxygen consumption and protein synthesis (fig. 3A,B) revealing vigorous metabolic activity--even in seeds which have not received a germination stimulus. With entry into skotodormancy, however, metabolic rates fall precipitously, and are maintained at a low level during many months of storage (fig. 3A,B). The lowered oxygen consumption is the result of an inherent change in the respiratory mechanism within the seeds, and is not a consequence of restrictions in oxygen permeability due to changes in the surrounding seed coat (Powell, A. D. and others 1984). Even as protein synthesis

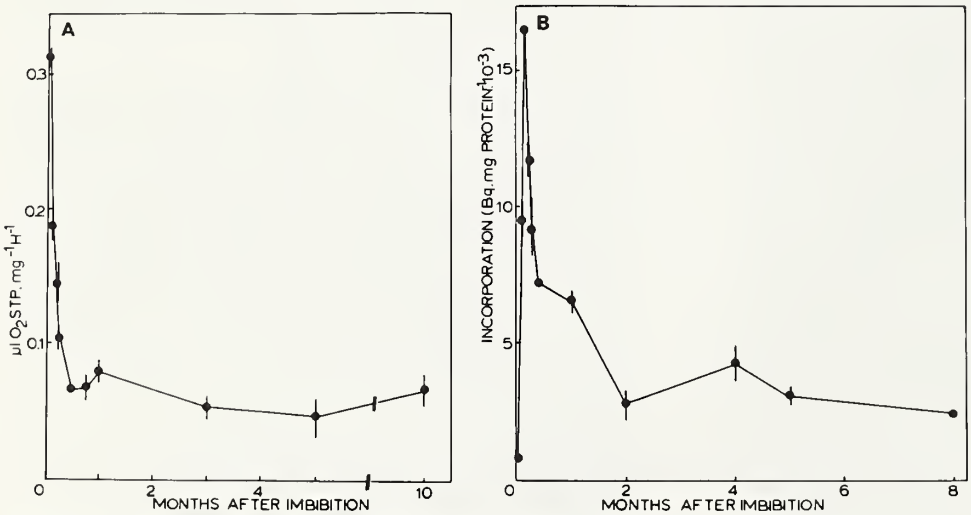

Figure 3.--Changes in (A) oxygen uptake and (B) incorporation of ^{3}H-leucine into protein by imbibed lettuce seeds stored in a dormant state for up to 10 months. After Powell and others (1983).

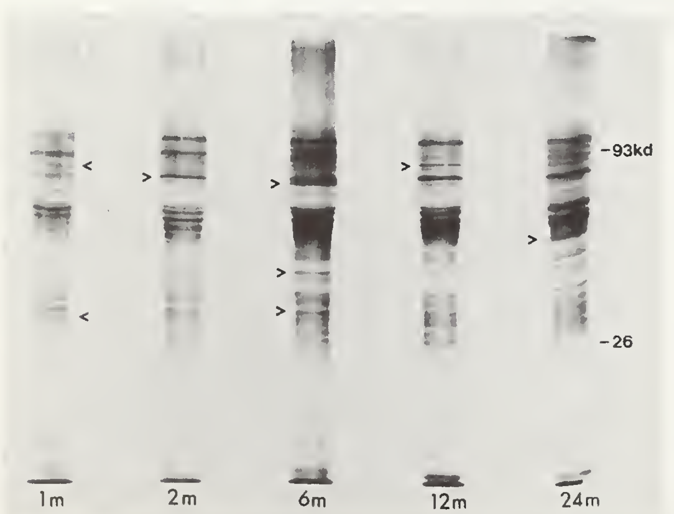

Figure 4.--Protein synthetic profiles of lettuce seeds stored imbibed in a dormant state for up to two years. Proteins were labelled with ^{3}H-leucine prior to extraction, separation by one-dimensional electrophoresis and preparation of the fluorograph. From Powell (1985).

declines there are only a few obvious changes in the actual proteins being synthesized (fig. 4). Presumably, then, the proteins required for the normal maintenance of the cells and the metabolic "well-being" of the seeds are produced in adequate amounts.

The energy for maintenance of metabolism in the skotodormant condition probably comes from utilization of the stored reserves within the lettuce cotyledons. Mobilization is relatively slow, with a decline in lipid and protein being approx. 20% and 25%, respectively, over a ten-month storage period (Powell and others 1983). Extrapolating such findings to the situation of seeds in the soil bank, it is possible that eventually the constraint on viability could be nutritional rather than a consequence of metabolic and/or structural deterioration. Such mobilization within seeds buried in the soil, however, would be at a much reduced level compared with that in the artificial conditions of high temperature and moisture used in the studies on lettuce seeds. Seeds achieving long-term viability in the soil would be subjected to generally lower temperatures, lower moisture contents, and intermittent drying, all of which could prolong the time over which the storage reserves would be retained.

Storage of seeds in the imbibed state may not be economically feasible if carried out on a large scale. The seeds must be maintained under constant temperature and moisture conditions; and contamination by fungi or other microorganisms must be prevented. Hence, they will require attention at regular intervals if the seed stocks are to be held in optimal conditions.

RECALCITRANT SEEDS: SPECIAL STORAGE PROBLEMS

There is a group of species that produce seeds which normally never dry out on the mother plant; they are shed in the moist condition and are killed if their moisture content is reduced below some relatively high critical value. Hence these seeds do not conform to the rules which can be applied to the orthodox group, and they have been called recalcitrant (Roberts 1973; Roberts and King 1980). Even when these recalcitrant seeds are stored under moist conditions their longevity may only extend from several weeks to several months. Included in the list of species that produce recalcitrant seeds is a number of large-seeded hardwoods (e.g. Corylus, Castanea, Quercus, Aesculus, Salix and Juglans), aquatic species, and a number of important tropical plantation crops such as Coffea, Cola, Theobroma and Hevea.

The inability to store seeds of recalcitrant species is a serious problem, for while vegetative propagation is possible for some species the retention of viable seed stocks is desirable in order to preserve maximum genetic diversity. While dry storage is obviously out of the question, other methods which are suitable for orthodox seeds are also undesirable, e.g. low-temperature storage is inappropriate for seeds of tropical plants, although for those of temperate woodland species it may be of value. Even within the same genus some seeds appear to be more sensitive to low temperatures than others, e.g. Shorea ovalis seeds have to be stored above 15°C, whereas S. talura seeds can be maintained at 5°C (Sasaki 1976).

Determination of optimal storage conditions for recalcitrant seed species is generally empirical, and little has been done to define the quantitative relationship between environmental parameters and viability. Perhaps an alternative strategy for storage, other than as the seed itself is appropriate. We noted earlier that large-seeded forest species can establish themselves as stunted seedlings on the forest floor under very low light conditions. Recalcitrant seeds normally possess a rapid and uniform germination strategy, with no dormancy. The seeds are generally large. Hence it may be appropriate to store recalcitrant species as seedlings or young plants, and not as seeds. As suggested by Hawkes (1980) research on recalcitrant seeds might best be directed away from seed storage problems, and towards seedling survival at low light intensities. The most appropriate soil and moisture conditions should be elucidated, the most efficacious intensity and quality of light determined, as well as the requirement for other specific factors (e.g. mycorrhizal associations). Methods for seed storage in soil, or even in culture tubes, could be devised, and it can be reasonably expected that many seedlings could be conserved per unit area as tubes of explants. Removal of seedlings from storage, accompanied by an increase in light intensity should lead to the resumption of normal growth. Work on Cryptomeria seedlings in culture has indicated that seedlings will survive for up to two years in a healthy condition at 10°C under short-day illumination (Isikawa 1978).

SUMMARY

Methods for seed storage are many, and diverse, but for orthodox seeds storage at low temperatures (0 to -20°C) and low moisture content (5-7%) seems to be satisfactory for most species. Such conditions are not particularly "natural" as far as the seed is concerned, but it seems well adapted, both structurally and physiologically to survive them. Problems with deterioration are exacerbated by poor storage conditions, but even in the dry state seeds undergo deterioration in a manner which cannot be combatted by their natural defence mechanisms, which appear to require hydration in order to be effective. For some seeds with a low viability in storage, or a low recovery rate of metabolism upon subsequent rehydration, there may be advantages in harvesting prematurely.

Many seeds persist naturally in the soil as seed-soil banks for long periods, and therein may be in at least a partially hydrated state for extended periods. Dormancy mechanisms ensure that full germination of the seed bank does not occur, and the slow release from dormancy,

usually following an appropriate environmental due is of advantage.

Recalcitrant seeds cannot be stored in conditions of low relative humidity, and many do not withstand a low temperature treatment. Little is known about the optimum conditions required for storing such seeds, but the use of seedling banks, rather than seed banks might be most appropriate. Such seedling banks might be considered for more widespread use for conservation of difficult forest species which do not exhibit dormancy mechanisms, and which do not persist in seed-soil banks, but which can survive under sub-optimal growth conditions.

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Section 1. Cone and Seed Biology

CONE AND SEED BIOLOGY

John N. Owens

ABSTRACT: The time between cone initiation and seed maturity of conifers from the Inland Mountain West varies from 16 to 27 months. Cone and seed production are affected at many stages during these long reproductive cycles. Eight patterns of cone initiation occur which help explain how environmental factors affect cone initiation and aid in timing cone induction. Four pollination mechanisms occur. Pollination at the optimal time for each pollination mechanism can significantly increase seed set. Most pre- and post-fertilization factors affecting cone and seed development are poorly understood but can affect seed production.

INTRODUCTION

Conifer reproduction begins with the initiation of reproductive buds after a variable period of juvenile growth. The time between cone initiation and seed maturity varies from 16 to 27 months. The reproductive cycles are well known for a few conifers from the Inland Mountain West but many details are not known for most species. Generalization may be made about species within a genus but exceptions may occur. Factors can promote or reduce cone and seed production at many stages during the long reproductive cycles. Little is known about many of these factors and how they affect seed or cone development. Understanding the reproductive cycles and the factors affecting development will help increase seed production and seed quality for reforestation. The purpose of this report is to describe the status of our knowledge of cone and seed development of conifers of the Inland Mountain West, point out areas where more research is needed and suggest some new approaches which might be used to study cone and seed development.

REPRODUCTIVE CYCLES

Matthews (1963) was the first to generalize that in temperate-zone trees reproductive buds are initiated in the growing season preceding the spring in which cones or flowers appear and anthesis occurs. This generalization has held over the years with few exceptions.

Reproductive buds undergo early development before winter dormancy and overwinter at various stages. During the second and in some species the third or fourth growing season variations occur affecting the length of the reproductive cycle. Three primary types of reproductive cycles represent the variation found in most conifers. Descriptions of many species are brief and include only a few aspects of the reproductive cycle.

The 2-Year Cycle

The most common reproductive cycle in conifers is represented in figure 1, depicting *Picea glauca* (Owens and Molder 1984c). Pollination occurs in the spring or early summer of the second year. The time between pollination and fertilization is brief, usually only a few weeks. Following fertilization, embryo and seed development are rapid and continuous. Seeds are mature and may be released as early as late summer the year of pollination. Retention of seed beyond that time is often determined by climatic or biotic requirements unique to a species and its method of seed dispersal.

Detailed descriptions of the complete reproductive cycles of conifers with this pattern are few and include *Picea* (Owens and Molder 1984c), *Pseudotsuga* (Allen and Owens 1972; Owens 1973), *Thuja* (Owens and Molder 1984a) and *Tsuga* (Owens and Molder 1984d).

The 3-Year-Cycle--I

A second reproductive cycle is found in most species of *Pinus*, and several other conifers. Unfortunately, this cycle is used in general textbooks as the "typical" conifer reproductive cycle (fig. 2). Pollination occurs in the spring or early summer of the second year, pollen tubes and ovules partially develop but then stop usually in mid-summer. Development resumes the following spring, fertilization occurs and embryos and seeds are mature in the fall. Seeds are usually shed in the year they

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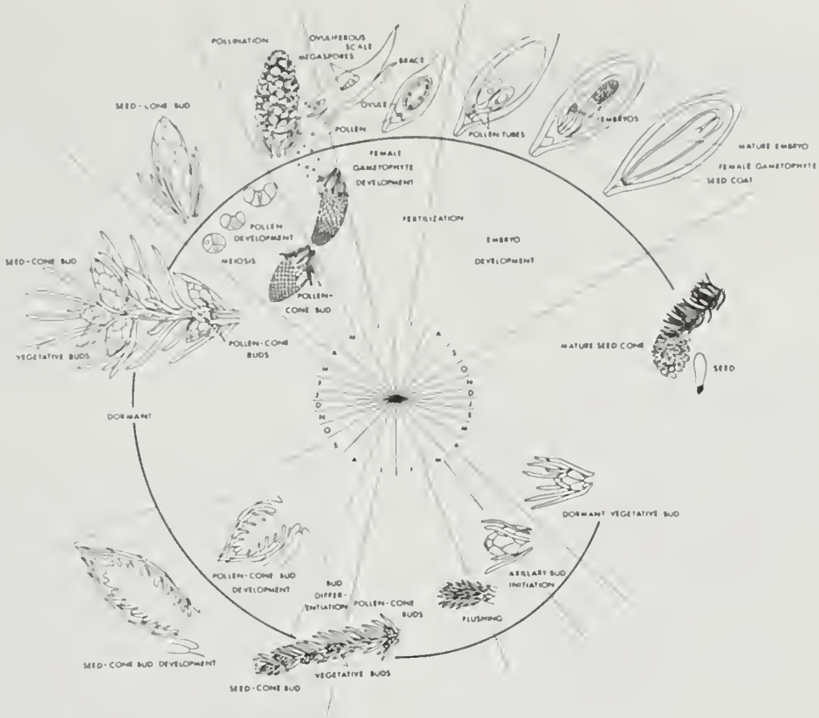

Figure 1.--The reproductive cycle of white spruce (Picea glauca) (from Owens and Molder 1984c).

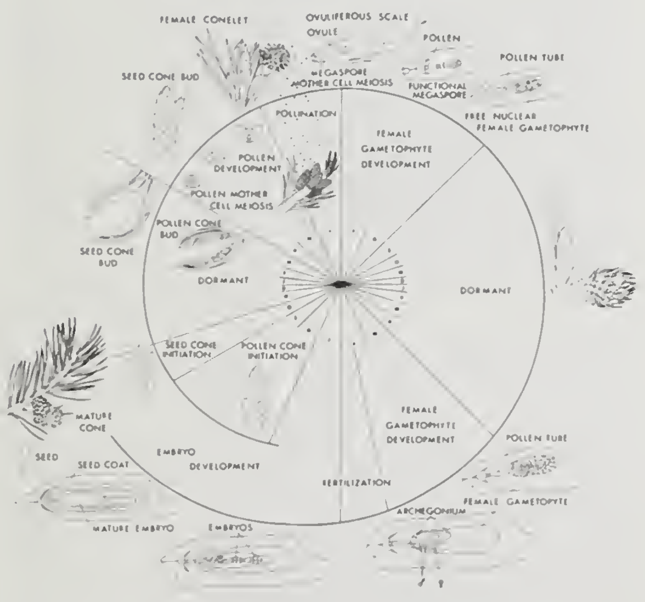

Figure 2.--The reproductive cycle of lodgepole pine (Pinus contorta) (from Owens and Molder 1984b).

mature. Serotinous seed cones may remain closed for many years before opening, commonly in response to extreme heat from fires, releasing many years of accumulated seeds at one time. This is a minimum 3-year cycle (commonly about 27 months) from reproductive-bud initiation to seed maturity. Complete descriptions of this type of reproductive cycle are limited to Pinus (Lill 1974; Owens and Molder 1984b). Similar life cycles are shared by a few other conifers from the northern hemisphere (e.g. Sequoia) and several from the southern hemisphere (e.g. Araucaria, Podocarpus) (Singh 1978).

The 3-Year-Cycle--II

A third reproductive cycle is found in a few conifers in the Cupressaceae. Pollination occurs in the spring or early summer of the second year, and fertilization occurs within a few weeks. Embryo and seed development begin but become arrested in late summer or fall. The seeds and cones overwinter in a dormant condition, then resume development in the spring of the third year (fig. 3). This reproductive cycle has been completely described for Chamaecyparis nootkatenis (Owens and Molder 1984a) and partially described for several species of Juniperus (Johansen 1950).

Variations of the Basic Cycles

General silvics (Fowells 1965) and seed manuals (Schopmeyer 1974) refer to the time between pollination and seed release. However, where this time extends over more than one year the reason is not given and it is usually uncertain if the extended cycle results from the second or third type of life cycle.

A combination of the two 3-year reproductive cycles occurs in Juniperus communis (Ottley 1909; Kötter 1931) and three species of Pinus (P. pinea, P. leiphylla and P. torreyiana) (Dallimore and Jackson 1966; Francini 1958). In J. communis cone initiation occurs before winter dormancy and pollination occurs the following

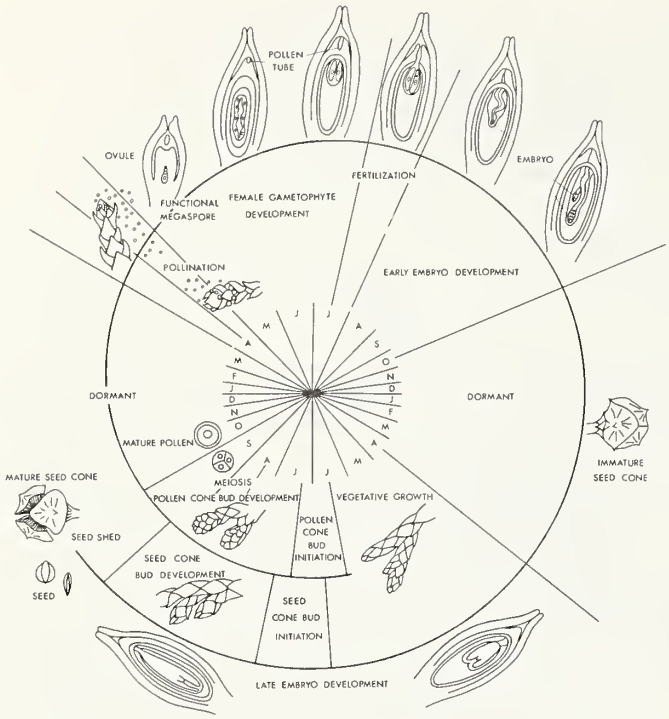

Figure 3.--The reproductive cycle of yellow cedar (Chamaecyparis nootkatensis) (from Owens and Molder 1984a).

spring. Pollen tube growth and ovule development become arrested and overwinter, with fertilization occurring in the third year. The immature embryos overwinter, then complete development during the fourth growing season. In the three species of pine, pollination occurs in the spring but pollen tube and ovule development remain arrested for two years. Fertilization, and embryo and seed maturation, occur in the fourth year.

In the long reproductive cycles there is tremendous scope for variation in the phenology, even though the sequence will remain unchanged. We must not assume that a species fits the textbook example, especially if we are attempting to control seed production. Also, as the length of the reproductive cycle increases so does the possibility of something going wrong. Therefore, it is not surprising that many species have rather low seed yields. To determine the causes of poor seed yield we must determine what went wrong at what stage of development.

CONE INITIATION

The time of cone initiation in the life of a tree and during the growing season may vary from one species to another as may the sites of cone buds in the crown and on the shoot. Understanding those variations is a prerequisite to understanding factors which affect cone initiation and for cone induction.

Cone buds are borne terminally or laterally (in axils of leaves) on the branch, and, except for the Cupressaceae, they are enclosed by bud scales. As a conifer reaches reproductive age seed cones are produced first, usually on vigorous lower order shoots, followed by pollen cones, usually on less-vigorous higher order shoots. There are several reviews of times and methods of cone initiation (Owens 1973, 1980; Puritch 1972; Owens and Molder 1977, 1979; Eis and Craigdallie 1981). Figure 4 is a summary of the most recent information. Several species from the Inland Mountain West have been studied and times and patterns within genera are usually similar.

Abies (true firs)

Several species have been studied including: A. amabilis (Ritchie 1966; Owens and Molder 1977a); A. balsamea (Powell 1974, 1977a, b); A. grandis (Owens 1984b); A. lasiocarpa (Owens and Singh 1982) and A. procera (Ritchie 1966). A summary is given by Owens and Molder (1985). Potential seed-cone buds are initiated in the axils of leaves on the upper surface of elongating primary or secondary shoots in the upper few whorls of the crown. Seed-cone buds occur most frequently on vigorous nodal shoots or on less-vigorous internodal shoots. Potential pollen-cone buds are initiated in the axils of leaves on the lower surface of elongating shoots in the mid- and lower regions of the crown. There is usually little overlap between seed-cone and pollen-cone bearing regions and seldom do the two types of cones occur on a branch. All axillary buds are initiated during early shoot elongation, at about the time of vegetative bud flush. Axillary buds do not become determined as pollen-cone, seed-cone or vegetative buds until the end of bud-scale initiation (fig. 5). Microsporophylls, bracts, ovuliferous scales,

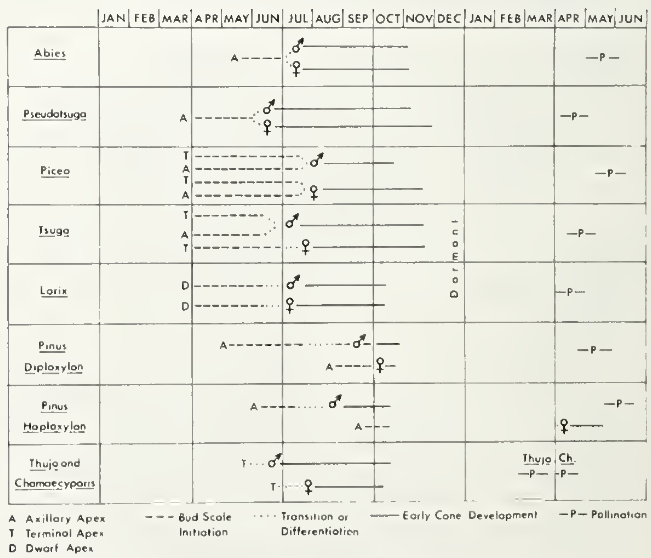

Figure 4.--Times and methods of cone initiation.

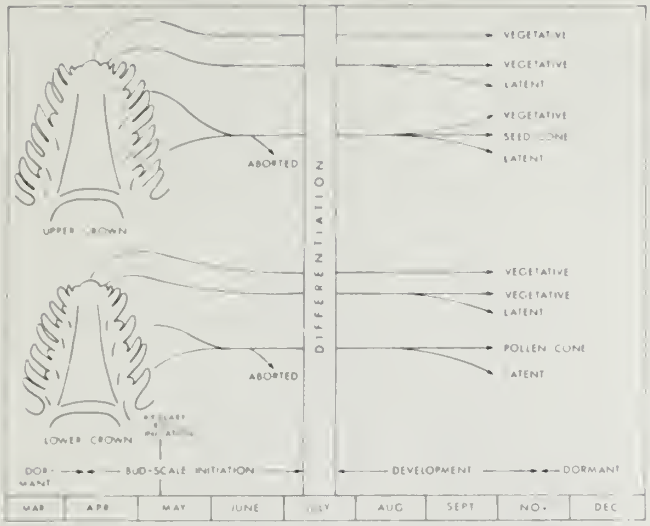

Figure 5.--Potential pathways of terminal and axillary bud development in Abies. Lower line shows vegetative bud development (from Owens and Molder 1985).

Figure 6.--Alternative pathways of axillary bud development in Douglas-fir (from Allen and Owens 1972).

and leaves begin to be initiated about mid-July. Pollen-cone buds complete development in about 2 months, whereas seed-cone and vegetative buds continue development into autumn. All microsporophylls, bracts, fertile ovuliferous scales and leaves are initiated before winter dormancy (fig. 4). In addition to the above three alternative pathways of bud development, axillary buds may abort during early development or become latent before becoming determined (fig. 5). Aborted buds often degenerate before forming many bud-scales, whereas latent buds initiate many bud scales and retain a living apical meristem capable of future growth.

Pseudotsuga (Douglas-fir)

Douglas-fir has been studied extensively (Owens 1969; Allen and Owens 1972). It is similar to Abies in most respects, except the position of cone buds is less rigorous. There is considerable overlap of seed-cone and pollen-cone bearing regions within the crown and both types of cone buds often occur on the same shoot. In the latter case, seed-cone buds are more distal. Both cone-bud types occur primarily on the lateral and lower surfaces of shoots. All axillary buds are initiated at the onset of vegetative bud growth and have initiated several bud scales before vegetative bud flush. The earliest stages of axillary bud determination can be recognized by using histochemical tests in early June (Owens 1969). All axillary buds become anatomically determined at the same time early in July, when lateral shoot elongation is nearly complete (Owens and others 1985). Microsporophylls, bracts and leaves begin to be initiated in early July. Pollen-cone buds complete development by late summer and become dormant early in the fall. Seed-cone and vegetative buds become dormant late in the fall (fig. 4). All microsporophylls, microsporangia, bracts, fertile ovuliferous scales, and leaves are initiated before buds become dormant. As in Abies, terminal buds rarely become reproductive and axillary buds may abort or become latent. In Pseudotsuga the number of cone buds which develop is determined not by the number of axillary buds initiated (although this does vary) but primarily by the proportion of these buds which differentiate into cone buds (fig. 6) (Owens 1969).

Picea (spruces)

The time and method of cone initiation has been determined for P. glauca (Fraser 1962; Eis 1967; Owens and Molder 1977e), P. engelmannii (Harrison and Owens 1983), P. mariana (Fraser 1966; G. Caron, personal communication) and P. sitchensis (Owens and Molder 1976) and is summarized by Owens and Molder (1984c). Spruce cone buds may develop from terminal apices which have been vegetative for one or more years or from newly-initiated axillary apices on elongating shoots (fig. 7). Except for the presence of terminal cones, cone distribution in the crown and on branches is similar to that described above for Pseudotsuga. In Picea engelmannii when cone buds are abundant, they occur mostly in the axillary but also in the terminal position. When cone buds are few (less than 35 percent of total buds) they are about equally distributed in terminal and axillary positions (Harrison and Owens 1983). This also appears to be true for P. glauca (Owens and Molder 1977e) and P. mariana (G. Caron, personal communication).

The time of cone-bud determination is remarkably similar for most species of Picea which have been studied. Cone buds become anatomically determined at the end of bud-scale initiation which occurs near the end of the period of lateral shoot elongation (Owens and others 1977; Owens and Molder 1977e; Harrison and Owens 1983; Dunberg 1979). Dunberg (1979) stressed that biochemical differentiation must occur before shoot elongation stops and anatomical differentiation begins. Pollen-cone, seed-cone and vegetative buds in terminal and axillary positions become determined at essentially the same time in all regions of the crown of a tree.

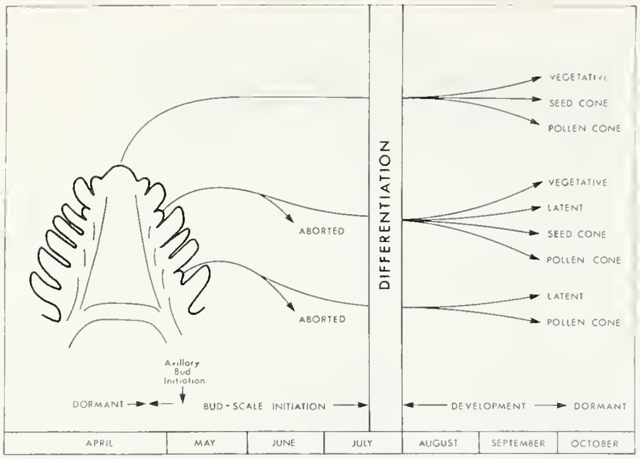

Figure 7.--Potential pathways of terminal and axillary bud development in *Picea*. Lower line shows vegetative bud development (from Owens and Molder 1984c).

In *P. sitchensis* (Owens and Molder 1976) and *P. glauca* growing at low elevations (Fraser 1958; Owens and Molder 1976, 1977e), bud determination begins about mid-July. In *P. engelmannii* growing at higher elevations determination begins in mid- to late July (Harrison and Owens 1983). The time of cone-bud determination within a species may vary with elevation and latitude, therefore provenance differences may be significant. Pollen-cone development is completed first, usually by late-September or early-October. Seed-cone and vegetative bud development may continue until mid-October in interior species (Owens and Molder 1977e; Harrison and Owens 1983) (fig. 4). All microsporophylls and microsporangia, bracts and functional ovuliferous scales, and leaves are initiated before buds become dormant (Owens and Molder 1984c). Axillary buds have the same potential pathways as in *Pseudotsuga* (fig. 6) and the abundance of cone buds is determined more by the pathways along which buds develop than by the number of axillary buds initiated. Terminal cone buds halt the future growth of a shoot and abundant terminal cones can reduce the cone-bud production and crown expansion of a tree.

Tsuga (hemlocks)

Only *T. heterophylla* (Owens and Molder 1974a) and *T. mertensiana* (Owens 1984a) have been studied and these are summarized by Owens and Molder (1984d). There is considerable overlap of seed- and pollen-cone buds in the crown and on branches. Seed-cone buds are terminal (some exceptions occur during cone-induction) and develop from apices which have been vegetative for 1 or more years. They form on vigorous lateral shoots in distal portions of branches. Pollen-cone buds usually develop from newly-initiated axillary buds on short lateral shoots in proximal portions of branches. They commonly form a cluster of buds at the base of the shoot but the terminal apex may also develop into a pollen cone. Cone position is essentially the same in both species (Owens and Molder 1984d). In coastal low elevation *T. heterophylla*, pollen-cone buds become determined in late June and seed-cone buds in mid-July (fig. 4). In coastal high elevation *T. mertensiana*, both pollen- and seed-cone buds become determined in late July (fig. 8).

Terminal, potential seed-cone apices have limited pathways of development--they may remain vegetative or differentiate into seed cone buds after bud scales are initiated. Axillary, potential pollen-cone buds may abort, become latent or differentiate into pollen-cone buds. In *T. heterophylla*, cone buds continue development until late fall, whereas in *T. mertensiana* development stops by mid- to late-October. All microsporophylls and microsporangia, bracts and functional ovuliferous scales are initiated before dormancy. Prolific terminal seed-cone development is common and may limit subsequent vegetative growth of the branch.

Larix (larches)

Larix has dwarf (short) and long shoot buds. *L. occidentalis* (Owens and Molder 1979b) and *L. laricina* (Powell and others 1984) have been studied in detail and the position of cone-buds is generally considered to be similar in other species of *Larix* (Dallimore and Jackson 1966). Pollen- and seed-cone buds normally differentiate from vegetative terminal apices on dwarf shoots that are at least 1-year-old (fig. 9). Occasionally cone buds develop from terminal-long-shoot buds on suppressed branches. Pollen-cone buds are commonly proximal on nonvigorous, often pendant, long shoots. Seed-cone buds are commonly distal on vigorous, but only slightly pendant to upswept long

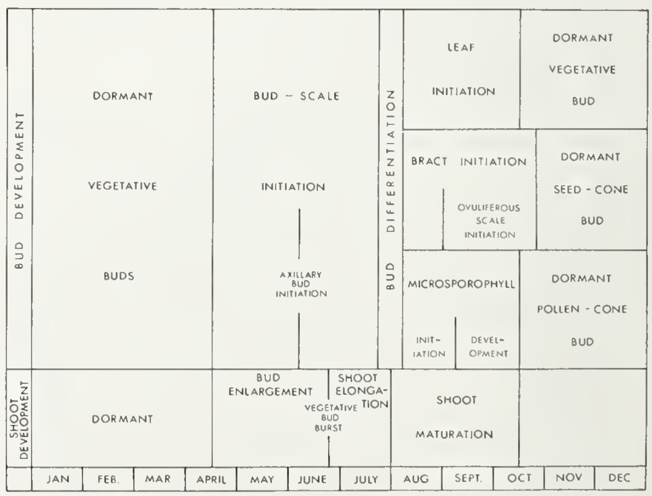

Figure 8.--Phenology of bud differentiation and development in mountain hemlock (redrawn from Owens 1984a).

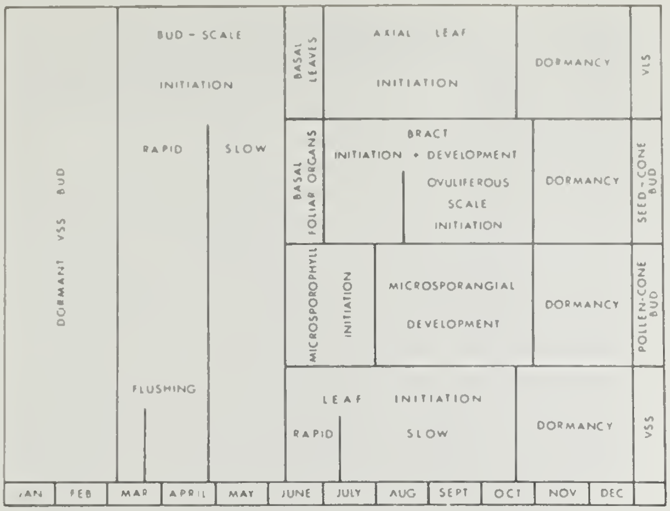

Figure 9.--Phenology of vegetative short shoot (VSS), long shoot (VLS), pollen-cone and seed-cone bud development in L. occidentalis (from Owens and Molder 1979b).

shoots. Considerable overlap occurs in distribution of cone-buds in the crown and along the branches (Owens and Molder 1979b). In L. occidentalis pollen-cone and seed-cone buds become determined in mid-June. Microsporophyll initiation is complete in about 6 weeks and is followed by microsporangial development. Bracts and ovuliferous scales are initiated until early November when both seed and pollen-cone buds become dormant (fig. 9) (Owens and Molder 1979b). Similar detailed studies have not been made for other Larix species. Related genera, Cedrus and Pseudolarix, within the Laricoideae of the Pinaceae have similar distributions of cones but details of development are not known.

Pinus (pines)

In pines, cone buds are initiated in a complex vegetative long-shoot bud (LSB) rather than on an elongating shoot or a dwarf shoot. The LSB consists of a series of scale leaves (cataphylls) which are initiated throughout the growing season. Most cataphylls have an axillary apex which initiates a series of bud scales, then differentiates into a dwarf shoot, pollen-cone or lateral LSB (fig. 10). Therefore, axillary bud initiation and differentiation occur throughout the growing season. The time when an axillary bud differentiates is determined by its position in the LSB--the proximal buds which were initiated first differentiate before the more distal axillary buds (Doak 1935; Sacher 1954; Duff and Nolan 1958; Owston 1969; Van den Berg and Lanner 1971; Sucoff 1971; Curtis and Popham 1972; Lanner and Van den Berg 1975; Owens and Molder 1975a, 1977b, c). LSB's may be monocyclic consisting of one complete sequence (fig. 10) or polycyclic consisting of two or more sequences.

Axillary buds are initiated at the base of the LSB in the spring or early summer. They initiate bud scales then differentiate into pollen-cone or dwarf-shoot buds during the summer. A more-distal group of axillary buds differentiate into dwarf shoots bearing the characteristic number of needles for the species. The most-distal axillary buds are initiated in late summer and after a period of bud-scale initiation, differentiate into either lateral long-shoot or seed-cone buds (fig. 10). In hard pine (diploxylon), lateral long-shoot and seed-cone buds differentiate in late summer or early fall in north temperate regions (Sacher 1954; Duff and Nolan 1958; Gifford and Mirov 1960; Van den Berg and Lanner 1971; Curtis and Popham 1972; Owens and Molder 1975a) (fig. 4). In soft pines (haploxylon), distal axillary primordia do not differentiate before the LSB becomes dormant. Immediately following dormancy they differentiate into either lateral LSBs or seed-cone buds (Sacher 1954; Owston 1969; Owens and Molder 1977b, c) (fig. 4).

In pines having polycyclic LSBs, more than one series of seed-cone buds may occur in a LSB but the first series usually bears most of the seed-cone buds (Lanner and Van den Berg 1975; Owens and Molder 1975a; Sweet 1979; Greenwood 1980). Polycyclic LSBs occur in many hard pines and are most common in those from southern latitudes. They have not been reported in soft pines.

Cupressaceae (cypress family)

The time and method of cone initiation has been determined only for Cupressus arizonica (Owens and Pharis 1967), Thuja plicata (Owens and Pharis 1971) and Chamaecyparis nootkatensis (Owens and Molder 1974b, 1984b). In the

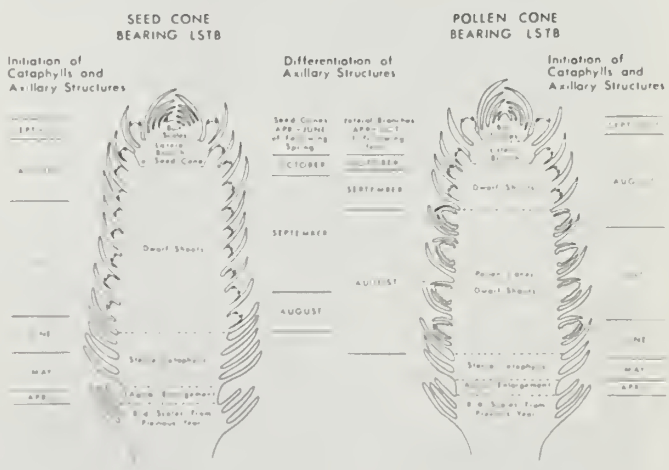

Figure 10.--The development of monocyclic LSBs of P. monticola. The columns on the left and right indicate the time of initiation and proportion of cataphylls and axillary structures initiated during this time. The center columns indicate the approximate times of differentiation of the axillary structures on each LSTB (from Owens and Molder 1977b).

Cupressaceae, cone buds form by the transition of a vegetative apex into a reproductive apex. Buds are not enclosed by bud scales. Seed cones are terminal on short lateral shoots located on distal portions of vigorous shoots. Pollen cones are terminal on proximal, less-vigorous lateral shoots. There is considerable overlap in cone distribution on branches and in the crown. Shoot elongation and leaf and axillary bud initiation occur over most of the growing season. Transition from a vegetative to a pollen-cone apex begins in early June in T. plicata, and in late June in C. nootkatensis. Transition to seed-cone apices follows in 4 weeks and 1 week, respectively (Owens and Pharis 1971; Owens and Molder 1974b, 1984a) (fig. 4). Only pollen cone initiation as a result of gibberellin A_3 treatments, rather than under natural conditions, was studied in Cupressus arizonica (Owens and Pharis 1967). In the Cupressaceae which have been studied, all microsporophylls and microsporangia, bract-scales and ovules are initiated before cone-buds become dormant in the fall.

FACTORS AFFECTING CONE INITIATION

Knowledge of time and method of cone initiation is useful in interpreting environmental or developmental factors which may affect floral initiation and in determining the correct time to attempt cone enhancement or induction.

Many studies have tried to demonstrate a relationship between environmental factors and cone initiation in regions, stands and individual trees (see reviews by Mathews 1963; Jackson and Sweet 1972; Puritch 1972; Lee 1979; Owens and Blake 1985). Correlation between seed crop and weather data are tempting. However, Rehfeldt and others (1971) cautioned that, "In any attempt to correlate previous cone crops and previous weather, problems arising from intercorrelations among the dependent and independent variables will be encountered; it is difficult to identify causal mechanism because of these intercorrelations."

Despite the problems, several factors have been identified. The very old concept that high summer temperatures favor increased floral initiation has been demonstrated in several conifer genera which grow in the Inland Mountain West, including Pinus (Maguire 1956; Daubenmire 1960), Pseudotsuga (Lowry 1966; Van Vredenburch and La Bastide 1969; Eis 1973), Abies (Eis 1973), Picea (Fraser 1958) and Larix (Yanagihara and others 1960). Increased light intensity through thinning has enhanced cone production in Pinus ponderosa (Barnes 1969) and Pseudotsuga (Reukema 1961). Photoperiod may effect sexuality of cones in P. contorta (Longman 1961), Tsuga heterophylla (Owens and Molder 1974a), Chamaecyparis nootkatensis (Owens and Molder 1974b) and Thuja plicata (Pharis and Morf 1967). Studies of moisture have given conflicting results primarily because times of cone-bud differentiation were not known. Generally moisture stress has enhanced seed cone initiation in Pinus monticola (Rehfeldt and others 1971), Pseudotsuga (Eis 1973; Lowry 1966), Abies grandis (Eis 1973) and Picea glauca (Fraser 1958). Frost resulting in lesions and girdling has increased cone production in Pseudotsuga (Ebell 1971).

The lack of positive correlations with environmental factors may result from endogenous factors within the trees. Cone-bud differentiation occurs during shoot elongation and maturation of subtending cones (Allen and Owens 1972; Owens 1984b) which are strong metabolic sinks (Ching and Ching 1962). No matter how favorable environmental factors might be, they rarely override the effects of bearing a heavy cone crop and consecutive heavy cone crops do not occur. Bumper crops may occur when endogenous and favorable environmental factors are in phase.

CONE INDUCTION

Cone induction in juvenile or otherwise non-reproductive conifers is a valuable tool in genetic tree improvement programs and in seed production for reforestation. Successful treatments are numerous and results variable depending upon the species, growing conditions and time of treatment. Any cone induction treatment must be applied before the time of anatomical differentiation of buds (fig. 4). How long before and for what duration are unknown for most species.

Various cultural treatments have been reviewed by Puritch (1972), Jackson and Sweet (1972), Brazeau and Veilleux (1976), Lee (1979) and Owens and Blake (1985). Successful treatments of genera from our region include: (1) fertilizers in hard pines (Lee 1979), soft pines (Schubert 1956; Barnes and Bingham 1963), Pseudotsuga (Ebell and McMullan 1970; Ebell 1972a, b) and Picea (Holst 1971); (2) girdling, banding and strangulation in Pseudotsuga (Ebell 1971) and Larix (Melchior 1960, 1961a, b); (3) moisture stress, usually applied by root pruning, in Pinus (Stephens 1961, 1964), Pseudotsuga (Melchior 1968; Ross and others 1985), Larix (Heitmuller and Melchior 1960) or withholding water in potted trees of Tsuga, Picea and Pseudotsuga; (4) growth of seedlings under continuous light to reduce the age to flowering in Picea (Young and Hanover 1976) and Pinus (Wheeler and others 1982); (5) altered photoperiod which may affect sexuality of cones in Pinus (Longman 1961), Picea (Durzan and Cambell 1979), Larix (Yokoyama and Asakawa 1973), Thuja (Owens and Pharis 1971) and Chamaecyparis (Owens and Molder 1977f); and, (6) shoot pruning in Pinus (Coffen and Bordelon 1981) and Pseudotsuga (Copes 1973). Many of these cultural treatments are most successful when used in conjunction with growth regulators.

About 100 research papers describe results utilizing a variety of species, growth regulators, concentrations of growth regulators,

times and methods of application plus several adjunct treatments. These are reviewed or tabulated by Owens and Blake (1985). The most successful treatments have used gibberellins (GAs). GA_3 was first shown to induce cones in some members of the Cupressaceae and Taxodiaceae in the late 1950's (Kato and others 1959). Since then 19 species in 10 genera within these families have responded positively to GA_3 treatments (Owens and Blake 1985). More recently less-polar GAs, usually a mixture of $GA_{4/7}$, have induced cones in 17 species of the Pinaceae representing five genera (Larix, Picea, Pinus, Pseudotsuga and Tsuga) (Owens and Blake 1985). Best results have been achieved when $GA_{4/7}$ was applied with some adjunct cultural treatment. Progress has been slower in the Pinaceae because: less-polar GAs are not as available and are more expensive than GA_3; treatments are not as easily applied (foliar sprays may not be effective); the timing of treatment is more critical since it must correlate with stages of bud development; the length of treatment may be longer (commonly 6 weeks or more); adjunct treatments are often necessary; and sexuality of cones is not easily manipulated. Much more research is needed on all of these problems in many species. Recent research on containerized (potted) rooted cuttings, grafts and seedlings (S.D. Ross, personal communication) shows promise for the development of containerized seed orchards of some species. Basic research on the mode of action of GAs must continue if cost-effective treatments are to be developed.

Most cone induction researchers are confident that seeds resulting from induced cones are comparable in quality to those from noninduced trees because cone induction treatments are of short duration and precede seed maturation by one or more years. However, excessive flowering can result in ovule, seed and cone abortion and perhaps seed of poor quality due to competition for resources. This may be especially true in small trees but may be most easily overcome in containerized trees.

CONE-BUD DEVELOPMENT

Seed-Cone Development

Seed cones of most conifers are preformed within the bud and any ovuliferous scales initiated after dormancy are sterile (Owens and Blake 1985). Exceptions occur in Pinus. In hard pines, one-third to all ovuliferous scales are initiated before winter dormancy, depending upon the position of the cone-bud on the shoot (Owens and Molder 1975a). In soft pines (see fig. 4). all bracts and ovuliferous scales are initiated after winter dormancy (Owens and Molder 1977b). We know little about the effect of overwintering conditions on seed-cone buds. Seed-cone buds resume development before vegetative buds, often during harsh late winter weather conditions. Cone-bud abortion is a common but poorly documented phenomenon in some species.

Pollen-Cone Development

Pollen cones initiate all microsporangia (pollen sacs) before winter dormancy (see fig. 4). However, the stage of microsporangial development reached before dormancy varies between genera (fig. 11). Overwintering may begin when pollen cones are at the sporogenous stage in Pinus (Kupila-Ahvenniemi and others 1978; Owens and Molder 1977c; Owens and others 1981b) or at the pre-meiotic pollen mother cell (PMC) stage as in Picea and Abies (Owens and Molder 1977d, 1979a; Singh and Owens 1981a, b; Harrison and Owens 1983). In these genera, meiosis and pollen development occur after winter dormancy. Ultrastructural studies of overwintering sporogenous cells of Pinus (Kupila-Ahvenniemi and others 1978; Cecich 1984) and PMCs of Pseudotsuga (Singh and others 1983) have shown that a true dormant period does not occur, rather nuclear and cytoplasmic changes occur throughout the winter. This period is more correctly called a period of reduced activity rather than dormancy. Similar studies have not been made for Abies or Picea.

In Larix, Pseudotsuga, Thuja and Tsuga, meiosis begins in the fall, then becomes arrested when PMCs reach either the pachytene or diffuse diplotene stages of meiosis (Eriksson 1968a; Eriksson and others 1970a, b; Owens and Molder 1971a, b; Hall 1982). After dormancy meiosis is rapidly completed, followed by pollen development.

In Chamaecyparis and Juniperus, meiosis and pollen development occur before winter dormancy (Owens and Molder 1974b). Overwintering pollen cones contain mature, dry pollen. No structural changes have been observed during winter.

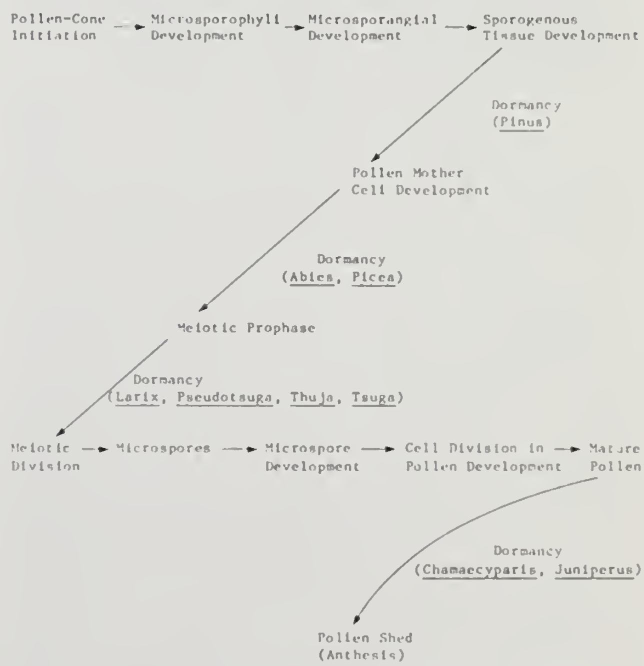

Figure 11.--Stages of pollen and pollen-cone development and times when dormancy may occur in different genera (from Owens 1982).

Winter temperatures and the stage at which pollen cones overwinter may affect pollen-cone buds and pollen quality (Eriksson and others 1970a). A higher incidence of pollen abnormalities occurred in Larix growing in Sweden, when PMC's developed beyond the diffuse stage before winter dormancy (Ekberg and others 1967; Eriksson 1968a, b). Consequently, trees moved to seed orchards in colder areas may have a higher incidence of pollen inviability or abnormalities.

Following meiosis, the tetrads of haploid microspores remain within the PMC wall for a brief time. They soon swell, burst out of the PMC wall and become suspended in fluid within the microsporangium where subsequent pollen development occurs (Singh 1978).

Two patterns of cell division occur during pollen development. In the Pinaceae (fig. 12A), prothallial cells form which have no known function. Pollen may be shed at the 4- or 5-celled stage. The body cell forms the two male gametes after pollination. Pollen is generally large, sacci (wings) are present in some genera and storage products are in the form of starch (Owens 1982; Owens and Molder 1971b, 1975b, 1977c, d, 1979a, b; Owens and others 1981b; Singh 1978; Singh and Owens 1981a, b).

In the Cupressaceae, Taxodiaceae and Taxaceae (fig. 12B), pollen has no prothallial cells and is shed at the 1- or 2-celled stage. The generative cell forms two male gametes after pollination. In these families, pollen is small, lacks sacci, is sculptured with orbicules and the storage products are oil droplets (Owens 1982; Owens and others 1980; Singh 1978).

The time sequence of meiosis and pollen development varies between species but can be separated into five stages of development: pre-meiotic division, meiotic division, microspore development, cell divisions, and anthesis. The time spent at each stage varies between species and with weather. The time from the end of pollen-cone dormancy to anthesis may be as little as 1 week in C. nootkatensis (Owens and Molder 1974b), to 12 weeks in Tsuga mertensiana (Owens and Molder 1975b). The effects of temperature on the rate of different stages of development are not known. However, increased temperatures will shorten the total time to anthesis (Sarvas 1962, 1965; Winton 1964; Boyer and Woods 1973) and forcing pollen for early pollen extraction is possible. Generally, the long period of post-meiotic pollen development makes it possible to control the rate of development in many species but the extent to which pollen can be manipulated before pollen development, vigor or viability are affected has not been determined.

POLLINATION MECHANISMS

'Pollination mechanism' is the term used to describe the process of pollen capture and entrance of pollen or pollen tubes into the ovules (Doyle 1945). The subject has been reviewed by Doyle (1945), Dogra (1964), Singh (1978), Owens (1980) and Owens and Blake (1985). All conifers are wind pollinated but differences occur in the pollination mechanisms.

Two mechanisms involving a pollination drop exist. In the Cupressaceae, Taxodiaceae and Taxaceae, ovules are flask-shaped with a narrow, short neck out of which a pollination drop is exuded. The pollination drop is a clear, dilute solution of sugars (McWilliam 1958). Conelets open in the spring exposing the ovules. Within a few days pollination drops are exuded from some of the ovules at night and withdrawn during the day for 2 or 3 days. Pollination drops then remain exuded throughout the day and night for a few days. This is followed by a few days when

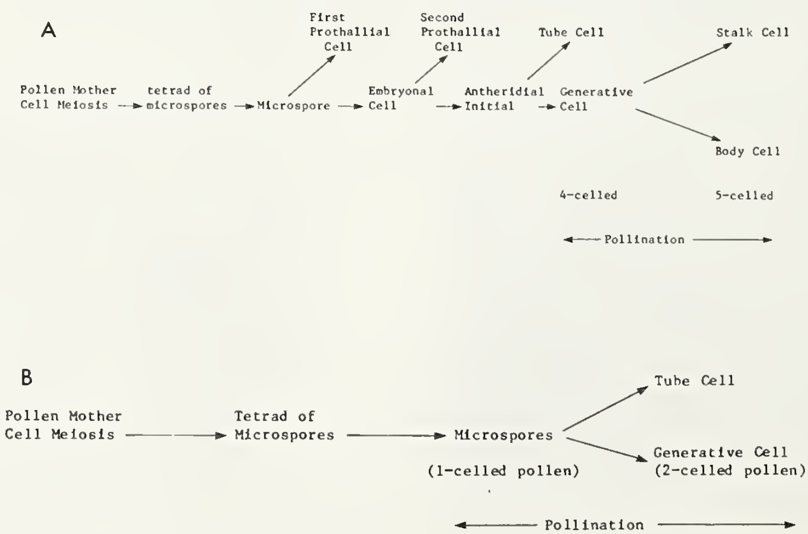

Figure 12.--A. Pollen development in Abies, Larix, Picea, Pinus, Pseudotsuga, and Tsuga (from Owens 1982). B. Pollen development in Chamaecyparis, Juniperus, Taxus, and Thuja.

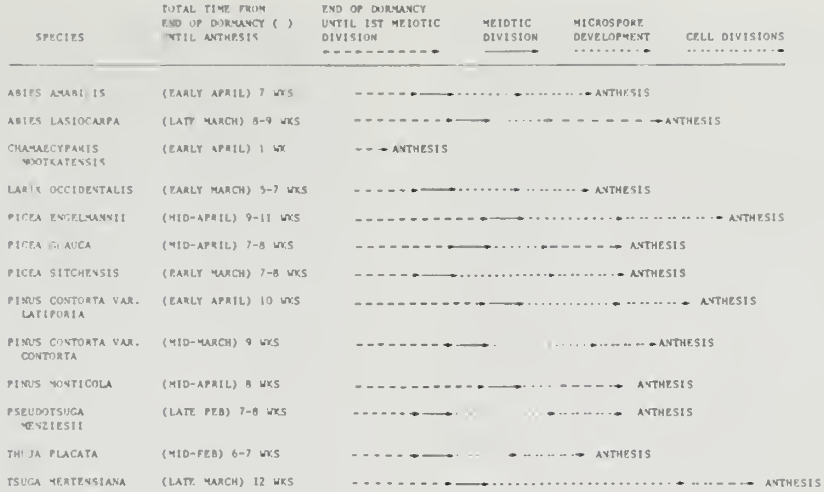

Figure 13.--Phenology of post-dormancy pollen-cone development in 13 conifers (from Owens 1982).

pollination drops are exuded only at night, then they are withdrawn permanently. Pollen landing on a pollination drop immediately sinks into the drop. Pollen adhering to the edge of the micropyle, before pollination-drop formation, is picked up by the pollination drop (Owens and others 1980).

A pollination drop is also exuded in Pinus and Picea but here the ovule is inverted and the ovule tip consists of two micropylar arms (McWilliam 1958; Lill and Sweet 1977; Owens and others 1981b; Singh and Owens 1981a; Owens and Blake 1984). The micropylar arms secrete minute sticky droplets to which pollen adheres for several days before a pollination drop forms. This provides a method by which pollen is collected and later taken in when the pollination drop floods the space between the micropylar arms (Owens and others 1981b; Owens and Blake 1984). McWilliam (1958) suggested that the pollination drop was produced by guttation but a recent study (Owens and Blake 1984) shows the drop is secreted by nectary-like tissue at the tip of the necellus.

In Abies the integument tip is funnel-shaped and lobed but no pollination drop forms (Owens and Molder 1977d; Singh and Owens 1981b). Minute droplets are secreted on the edge and inner surface of the funnel to which pollen adheres. The funnel then crimps inward carrying pollen closer to the nucellus.

Two pollination mechanisms occur in Tsuga. In the more primitive T. mertensiana, the two micropylar arms are broad flaps which secrete minute droplets to which pollen adheres. The flaps collapse, entrapping pollen grains which germinate, forming pollen tubes that grow into the micropyle (Owens and Blake 1983). In T. heterophylla, pollen has spines which adhere to long web-like cuticular hairs on the abaxial surface of the bract. After the ovuliferous-scales overgrow the bracts, the pollen grains germinate and form very long pollen tubes that grow over the bracts and into the micropyles of ovules of more distal ovuliferous-scales (Colangeli and Owens 1984).

In Pseudotsuga (Allen 1963; Ho 1980; Owens and others 1981a) and Larix (Owens and Molder 1979c; Villar and others 1984) the stigmatic tip develops into two unequal lobes covered with unicellular stigmatic hairs, and the micropyle is a narrow slit, too small for pollen to enter. Pollen sifts between the bracts of erect conelets and becomes entangled in the stigmatic hairs. This occurs for several days, then cells around the micropyle collapse and cells on the surface of the lobes elongate, carrying stigmatic hairs and attached pollen into the micropyle. Complete engulfment of stigmatic hairs occurs within about 2 weeks. There are no secretions on the stigmatic hairs and no pollination drops.

The optimal time for pollination and the duration of effective pollination vary for maximum seed yield with the pollination mechanism. In species having a pollination drop, most effective pollination occurs when the pollination drop is present (Owens and others 1981b; Owens and Blake 1984). However, in those that secrete microscopic droplets on the micropylar arms, pollen is also effectively collected on the micropylar arms. Experiments with Pinus (Owens and others 1981b) and Picea (Owens and Blake 1984) using stained pollen applied at various times show that some of this early pollen which adheres to the arms is taken into the ovule, but the most effective pollination occurs when the ovule has an exuded pollination drop. In these studies, and more recent studies of P. glauca (J.N. Owens, unpublished data), it was shown that not all ovules in a cone exude pollination drops simultaneously. Exudation occurs over several days and progresses acropetally in the cone. Therefore, different regions of each cone are most receptive at different times. This has obvious implications for controlled and

supplemental pollinations and implies that maximum seed efficiency in the field may occur when pollen arrives at the conelets over several days.

Experiments using stained pollen applied at different times throughout the receptive period show that, in Pseudotsuga, pollen is accumulated over several days and the most effective time for pollination is within about 4 days from when conelets first become receptive (Ho 1980; Owens and others 1981a). The first pollen to arrive at the stigmatic surface is taken into the ovule preferentially over pollen arriving later (Owens and Simpson 1982). In Picea glauca that was pollinated at different times with colored pollen, the pollen applied early was also most likely to be taken in and accomplish fertilization (R. Ho, personal communication).

Other pollination mechanisms which rely on a collection process (Abies and Tsuga) may have long receptive periods without optimal times. This has been demonstrated in T. heterophylla where each day for more than two weeks, previously unpollinated cones were pollinated, but the seed set was essentially the same for all dates (Colangeli and Owens 1984).

POST-POLLINATION FACTORS AFFECTING CONE AND SEED DEVELOPMENT

The time between pollination and fertilization is variable according to species (figs. 1-3). During this period seed cones rapidly enlarge and increase in dry weight (Ching and Ching 1962), ovules enlarge and female gametophytes mature (Owens and Blake 1985). After fertilization embryos and seeds develop. Both endogenous and exogenous factors may affect ovule, seed and cone development but these factors are poorly understood (Owens and Blake 1985).

Cone Abortion

Conelet abortion at and soon after pollination is common and thought to be primarily caused by low temperatures (Hard 1963; Hutchinson and Bramlett 1964; Krugman 1966), although there have been no experimental studies to prove this (Owens and Blake 1985). Death of the conelet commonly begins in the cone axis (White and Knopp 1978) and ovules, followed by wilting and browning of the bracts. Most studies of conelet loss have used Pinus, where this can usually be traced back to inadequate pollination. Sarvas (1962) estimated that 80 percent of conelet drop in P. sylvestris resulted from inadequate pollination and the remaining 20 percent resulted from damage to the conelet. He also estimated that when more than 20 percent of potentially fertile ovules aborted (due to lack of pollen) the conelet aborted. Strong clonal differences in amount and timing of conelet drop occur in Pinus (Sweet and Thulin 1969; Forbes 1971). Sweet (1973) and Owens and Blake (1985) provide complete reviews of the limited literature in this area. Generally, the physiology of conelet drop is poorly understood but the ability to induce cones on small containerized trees now makes experimental studies possible.

Post-fertilization cone loss has been reported (Brown 1970; Bramlett 1972) but is not common. Rehfeldt and others (1971) described this in P. monticola and showed it to be influenced by early summer water deficit. Sweet (1973) suggested the low cone loss at this time was due to less competition for nutrients since seeds and cones have approached full size by the time of fertilization. The seed coat is well developed at fertilization and seeds and seed wings have usually separated from the ovuliferous scales. No vascular connections exist between seed and cone at this time (Owens and others 1982; Singh and Owens 1981a, b, 1982) and seeds would no longer be strong metabolic sinks.

Prefertilization Factors Affecting Seed Development

The site and time of pollen germination vary. In Tsuga heterophylla very long pollen tubes grow into the micropyle (Colangeli and Owens 1984). In Pinus and Picea the pollination drop draws pollen to the nucellar tip where it soon germinates (Sarvas 1968; Owens and others 1981b; Owens and Blake 1984). In Abies (Owens and Molder 1977d; Singh and Owens 1981b, 1982) pollen germinates in the short micropylar canal near or on the nucellus. In Larix and Pseudotsuga, engulfed pollen elongates down the micropylar canal but a narrow pollen tube does not form until contact is made with the nucellus (Owens and Molder 1979c; Allen and Owens 1972). In all but Pinus and Picea there is considerable time between pollination and pollen germination but the stimulus for germination (or its inhibition) are not known. Many factors could prevent or retard pollen germination and pollen tube growth which would reduce seed set.

Pollen tube growth through the nucellus may take as little as one week in Pseudotsuga (J.N. Owens, unpublished data) to one year in Pinus (Sweet 1973). Competition between pollen tubes may occur during this period. The mechanisms which control pollen tube growth and penetration of the nucellus are not known. These aspects of conifer reproduction have not been studied.

Interractions may occur between pollen and pollen tubes and the nucellar and female gametophyte tissues. Such systems have been extensively studied in flowering plants but intraspecific prezygotic self-incompatability has not been reported in conifers (Hagman 1975). However, recent data shows that up to 20 percent of failure to set seed occurs before fertization (A. Colangeli, personal communication). Pettitt (1977a, b, 1979, 1982) has detected proteins ad glycoproteins in the pollen wall of the primitive gymnosperm Cycas and has demonstrated inter-species and

inter-tissue precipitation reactions between various components of ovular tissues. This suggests that proteins could be important in prezygotic incompatability during pollen germination and pollen tube growth through the nucellus, megaspore wall and female gametophyte, all of which are genetically different from the pollen. Seriologically active substances have been demonstrated in Pinus pollen (Hagman 1975) and immunochemical differences have been detected in female gametophytes of different P. strobus trees (Eckert and Eckert 1984).

These observations indicate that prezygotic stages of development have a potentially great effect on seed set. Consequently, we have embarked on a light and electron microscopy study of pollen tube growth and interspecific pollen competition using controlled pollinations of ^{14}C labelled pollen in Tsuga heterophylla, Picea glauca and Pseudotsuga menziesii. In addition, immunocytochemical techniques are being developed to study specific proteins produced by pollen tubes in Picea.

Deficient ovules may result from ovule abortion or lack of ovule development. All cones have ovuliferous scales at the base, and to a lesser extent at the tip, which bear either no ovules or rudimentary ovules. Rudimentary ovules either do not fully develop or develop too slowly to be pollinated (Owens and others 1981a, b). This is most obvious in some species of Pinus where the majority of scales bear no fertile ovules (Sarvas 1962; Owens and others 1982). Deficient ovules also occur in fertile regions of cones but this has not been carefully studied with regard to cause or frequency within cones, trees or species. Whatever the causes, deficient ovules can significantly reduce viable seed set.

Postfertilization Factors Affecting Seed Development

The literature on conifer embryogeny is extensive and most genera have been described (Roy Chowdhury 1962; Owens and Blake 1985). Since most conifers are multiarchegoniate, more than one egg may be fertilized and resultant proembryos develop at about the same rate. Fertilization of one egg in a female gametophyte does not appear to prevent subsequent fertilization of other eggs; however, unfertilized eggs rapidly degenerate as adjacent embryos develop. The fertilization of more than one egg, simple polyembryony (SPE), is common but not universal. The resulting embryos have different genotypes. Rarely does more than one proembryo develop into an embryo.

The proembryo stage ends when suspensor cells force the apical cells into the female gametophyte. Cells of the apical tier divide and may form a single embryo or separate into four filaments, each of which may develop into a separate embryo. This is called cleavage polyembryony (CPE) and the embryos are genetically identical.

Embryo development may continue normally (figs. 1, 2), be inhibited but resume development when conditions are favorable (fig. 3), or the embryos may degenerate. Degeneration has been traced to physiological incompatability between embryos and the female gametophyte as a result of self-pollination in Pinus (Hagman and Mikkola 1963), Pseudotsuga (Orr-Ewing 1957), and Picea (Mergen and others 1965). In other conifers such as Abies (Sorensen 1982) self-pollination does not lead to embryo degeneration. It has generally been thought that selection against selfing occurs by low self-embryo viability (Sorensen 1982) and that selection occurs during the post-zygotic stages (Willson and Burley 1983). Some of these concepts may need to be re-evaluated after prezygotic stages have been thoroughly investigated.

Irregularities in embryogeny have been demonstrated (Dogra 1967; Owens and Blake 1985) but their frequency, causes and final impact on seed set are generally not known. Dogra (1967) observed that the occurrence of any one irregularity may not be common but all together they played a significat role in seed sterility. Unfortunately, large samples and numerical data are generally lacking for embryological studies. Embryo retardation and abortion are common but the causes must be studied during development rather than after seeds are mature. Classes of normal appearing seeds have been described based on the condition of female gametophyte and embryos (Dogra 1957; Owens and Blake 1985). This approach, but with emphasis on the causes, should be applied to more conifers.

Seed and Cone Maturation

Seed and cone maturation have not been thoroughly studied developmentally or physiologically. Most studies have dealt with assessing the time of cone collection which is the subject of the next session. Only a few comments relate to the present topic.

Changes within the female gametophyte and embryo during seed development have not been well described for conifers (Owens and Blake 1985). One of the most complete studies was that of Ginkgo (Favre-Duchartre 1956, 1958), a primitive gymnosperm with seeds similar to conifers. Similar but less complete studies have been made for the Pinaceae (Hakansson 1956; Takao 1960). Hakansson (1956) followed embryo development and the state of food materials in the female gametophytes of Picea and Pinus and Simola (1974) made an ultrastructural study of the embryo and female gametophytes in dry and germinating seeds of P. sylvestris. Many more complete developmental and physiological studies are needed.

SUMMARY

Cone and seed biology of conifers is a broad subject, the species are many but the researchers are few. Cones and seeds are

essential for reforestation but many factors often prevent their production. These factors are generally poorly understood. Cone and seed production can be significantly increased for many species by cone induction or enhancement treatments and improved pollination techniques. Many factors are difficult to control but warrant further study. These include factors which prevent fertilization, cause ovule and embryo retardation and abortion and cause the abortion of cones. Much of the technology is now available to significantly increase cone and seed production in many forest trees. However, further research is required to refine the technology and provide basic information about conifer reproductive development and physiology.

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IDAHO WESTERN REDCEDAR (THUJA PLICATA DONN.) CONEBEARING STATUS IN AN UNUSUALLY DRY YEAR

William R. Gall and Allen S. Rowley

ABSTRACT: Twenty-six 1/5 acre (0.0809 hectare) plots were measured in western redcedar (Thuja plicata Donn.) stands in northern Idaho in 1979. Each plot represented one stand. Half of the plots contained western redcedar which were bearing cones of the current year, or cones that matured in 1978. The western redcedar stands bearing cones had a mean cedar d.b.h. of 11.4 inches (29 cm) versus 13 inches (33 cm) for nonbearing stands. Conebearing stands contained less basal area for the stand and western redcedar and more basal area of grand fir (Abies grandis), and western hemlock (Tsuga heterophylla). Conebearing stands had a mean elevation of 3120 feet (1125 m), and contained reproduction consisting of some combination of grand fir, western redcedar, and western hemlock; nonbearing stands were lower in elevation and had reproduction of western redcedar only and occasional Douglas-fir (Pseudotsuga menziesii).

Total height of two dominant or codominant cedars had a correlation of 0.694 with d.b.h. in conebearing stands; a larger value was found in nonbearing stands. The ratio of total height/d.b.h. had a correlation of 0.751 with the number of stems/ha and 0.751 with the number of cedar stems/ha in nonbearing stands. No significant correlation with these variables was found for conebearing stands.

INTRODUCTION

This study originated to obtain preliminary information about variation in the natural western redcedar (Thuja plicata Donn.) stands, including information about the reproductive biology of western redcedar in Idaho. Knowledge of this kind is necessary for planning a forest tree improvement program in any species or for deciding the need for a tree improvement program and to what extent the program would be worthwhile.

Currently little is known about the reproductive biology and natural variation of western redcedar in Idaho. Owens and Pharis (1971) described the phenology of western redcedar pollen and ovulate strobilus initiation, meiosis, and pollination in coastal British Columbia. Ebell and Schmidt (1964) reported on the effect of climatic conditions on western redcedar pollen release on Vancouver Island.

MATERIALS AND METHODS

Plant Materials

Twenty-six 1/5 acre (0.0809 hectare) plots were laid out in 1979 within the natural distribution of western redcedar in Idaho. Half of the plots contained western redcedar which were bearing cones that matured in 1978 or would mature in 1979. Representative stands were chosen on relatively dry sites or moist, well-drained sites; cedar bogs were avoided. Stands with a closed canopy and of approximately 50 percent cedar and a mean d.b.h. of 12 inches (30 cm) were chosen. Diameter at breast height was measured for all trees on the plot with a diameter of 3 inches (7.6 cm) or larger. Basal area was calculated accordingly for all the trees. No increment cores were taken to provide an estimate of age.

The total height of two dominant or codominant cedar trees was recorded. The western redcedar trees were scrutinized for cones with an 8 x 26 pocket monocular.

All trees between 7.6 and 15.0 cm d.b.h. were considered to be reproduction. If any tree species or a combination of any three tree species was represented by 10 or more trees in that diameter class in a plot, that species or combination of species was considered to be reproducing.

Environmental Variables

Elevation, latitude, and longitude of each stand were obtained from either a 7 1/2' or 15' topographic quadrangle map. Aspect of each stand was observed with a hand held compass. Weather data were obtained from the National Climatic Data Center (1977, 1978, 1979).

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Statistical Analysis

It was planned that data would be analyzed according to this analysis of variance:

n	Source of Variation	d.f.
2	Conebearing Status	1
13	Stands/Conebearing Status	24
t	Trees/Stands/Conebearing Status	1874
1900	Total Variation	1899

However, when analysis was begun it was observed that means for the two groups were sometimes very similar, and variation among stands within conebearing status sometimes obscured variation between the two kinds of stands. The exceptions were: percent cedar by number of stems and by basal area, total number of stems, number of cedar stems, 2-tree total height, 2-tree d.b.h. and 2-tree total height/d.b.h. A two-tailed F test (Snedecor and Cochran 1980) showed that the variance estimates for cedar basal area, plot basal area, cedar mean d.b.h., plot mean d.b.h., grand fir (*Abies grandis*) basal area, and western hemlock (*Tsuga heterophylla*) basal area were heterogenous. Therefore, it would not be appropriate to combine such variables into a single analysis as above. Instead, these variables were analyzed according to the following analysis of variance by conebearing status:

n	Source of Variation	d.f.
13	Stands	12
t	Trees/Stands	13(t-1)
	Total Variation	

Percent cedar by number of stems and by basal area were tested for skewness and kurtosis and found to be normally distributed. These two variables and total number of stems/acre and number of cedar stems/acre were analyzed according to this analysis of variance:

n	Source of Variation	d.f.
2	Conebearing Status	1
13	Stands/Conebearing	24
26	Total Variation	

Correlations were computed by conebearing status among cedar basal area, plot basal area, cedar d.b.h., plot d.b.h., number of cedar stems, total number of stems, 2-tree total height, 2-tree d.b.h., and 2-tree total height/d.b.h. Elevation was analyzed by a 2-way Chi-square test.

RESULTS

Conebearing status was found not to be independent of high and low elevation by a Chi-square test (table 1). Nonbearing stands occurred mostly at lower elevations below 3500 feet (1067 m). Conebearing stands were more variable but occurred most often at higher elevations. The stands were located from 46° 9' N to 48° 50' N and from 115° 37' W to 117° 2' W. No significant effect of the stands' location or aspect was found.

Table 1.--Number of stands in eight elevation intervals by conebearing status

Elevation Class (m)	Number of Conebearing Stands	Number of Nonbearing Stands
LOW		
457-609	0	1
610-762	0	1
762-914	3	3
914-1066	3	6
HIGH		
1067-1219	3	0
1219-1371	1	1
1372-1524	1	0
1524-1676	2	1
	13	13

Chi-square[1] = 4.25
d.f. = 1

[1]Indicates the probability of a greater Chi-square is less than 5 percent.

The field measurements define a difference in stand composition between stands bearing cones and those without cones. Table 2 displays the means of several variables for the two types of stands. The conebearing stands had less basal area for the whole stand and less western redcedar basal area. Conebearing stands did have a higher amount of basal area for grand fir, which occurred in 21 stands, 10 bearing redcedar cones. Also as seen in table 2, more basal area of western hemlock was found in conebearing stands where it existed in 12 stands, six bearing cones. Notice that the means of the two dominant tree heights were the only variables at all similar.

Table 2.--Means for selected variables by conebearing status

Variable	Conebearing	Nonbearing
Redcedar Basal area (m^2/ha)	5.16	9.99
Grand fir Basal area	3.10	1.42
Western hemlock Basal area	2.32	0.55
Total plot Basal area	10.49	13.80
Plot d.b.h. (cm)	25.9	33.0
Redcedar d.b.h.	29.0	33.0
Total height for dominant redcedar trees (m)	25.9	26.5
Stems/ha	865	919
Redcedar stems/ha	450	526

Counts of stems between 7.6 and 13.0 cm (3.0 and 5.9 inches) were used to quantify reproduction, although in shade-tolerant species d.b.h. may not be well correlated with age. Any species or combination of any three species having 10 or more stems in this d.b.h. class was arbitrarily considered to be reproducing on that plot. In some stands no stems of any species were present in this size class in sufficient numbers to qualify as reproduction. In conebearing stands reproduction consisted of cedar, grand fir, or western hemlock, singly or in a combination. In nonbearing stands reproduction consisted of cedar alone in five stands, along with Douglas-fir

(*Pseudotsuga menziesii*) or western larch (*Larix occidentalis*) in two stands.

Table 3.--Tree species of reproduction size (10 stems or more between 7.6 and 15.0 cm d.b.h.) by conebearing status of stands

Conebearing Stands		Nonbearing Stands	
Stand No.	Species Reproducing	Stand No.	Species Reproducing
9	grand fir	7	cedar
10	cedar	8	cedar
11	cedar and hemlock	16	
12	cedar and hemlock	17	cedar
13	cedar, hemlock and grand fir	18	
14	cedar and hemlock	19	cedar
15		20	cedar
22	grand fir	21	cedar and Douglas-fir
23	cedar and grand fir	24	cedar and larch
28		25	
29	cedar	26	
30		27	cedar
32	cedar and grand fir	31	

Variance estimates among conebearing and nonbearing stands were found by a two-tailed F test to be heterogenous for cedar basal area, plot basal area, cedar mean d.b.h., plot mean d.b.h., western hemlock basal area, and grand fir basal area (table 4). The variance estimates were larger in conebearing stands only for grand fir and western hemlock basal area.

Table 4.--Two-tailed F values for selected variables by conebearing status

Variable	Conebearing	Nonbearing
Plot mean d.b.h.	([1])	7.249**
Plot basal area		17.007**
Cedar mean d.b.h.		3.667*
Cedar basal area		25.165**
Stems/acre		2.098 n.s.
Cedar Stems/acre	2.236 n.s.	
Western hemlock basal area	8.589**	
Grand fir basal area	4.442**	

[1]Each F ratio is listed under the type of stand with the largest variance estimate.

**Indicates the effect was significant at P<1%.

*Indicates the effect was significant at P<5%.

n.s. Indicates the effect was not significant at P<5%.

Correlation coefficients among variables were calculated for conebearing stands and are presented in table 5. For conebearing stands the ratio two-tree mean total height/d.b.h. was not significantly correlated with any other variable. In nonbearing stands the two-tree mean total height/d.b.h. ratio was only significantly correlated (P<1%) with the number of stems/acre and number of cedar stems/acre. Two-tree mean d.b.h. was significantly correlated with plot mean d.b.h. and cedar d.b.h. (P<1%) and with plot basal area, cedar basal area and number of stems/acre (P<5%).

Variance estimates for the ratio total height/d.b.h. between conebearing and nonbearing stands were not heterogeneous by a two-tailed F test (P<5%), and the effect of conebearing status was not significant in the analysis of variance.

Relative amounts of among-stand and within-stand phenotypic variation are given in table 5 for the total height/d.b.h. ratio by conebearing status. Among-stand variation was larger than within-stand variation in both conebearing categories. These figures are based on a separate analysis of variance computed by conebearing status for the ratio of total height to d.b.h.

DISCUSSION

Conebearing stands were more common at higher elevation. Habeck (1979) reported that climax western redcedar stands in the Selway-Bitterroot Wilderness in Idaho were reproducing at higher elevations but not at lower elevations. In spite of the fact that Fowells (1965) called western redcedar a prolific seeder, Gashwiler (1969) said that seedfall of western redcedar in west central Oregon over a period of 12 years was erratic. As a possible explanation for these observations Ebell and Schmidt (1964) report a strong climatic effect on pollen production in western redcedar. For the cones observed in this study weather or elevational moisture differences could have been a factor.

The winter of 1977-78 was drier than normal. The months of January through April were 25 percent below normal for precipitation recorded at weather stations in Idaho. This time period is also a key time for western redcedar reproduction as meiosis followed by pollination is occurring (Owens and Pharis 1971). The cones we observed in 1979 were undergoing meiosis and pollination during this dry period. During a dry winter in 1938-39 in Illinois Martin (1952) found that the sporophylls and microsporangia of northern white cedar (*Thuja occidentalis* L.) became desiccated. The desiccation accounted for a low rate of survival of staminate cones. Similarly the dry winter of 1977-78 could have produced the same effect in the stands we examined.

The fact that the correlation of d.b.h. and total height is different and smaller for means of conebearing than nonbearing stands suggests the two variables can be manipulated somewhat independently. Wright (1975) reported that measurement of Scotch pine (*Pinus sylvestris* L.) plantations in Michigan after 12 growing seasons in the field showed that there are general genes for growth rate, as well as specific genes for height and diamater growth. If improvement is to be made in the ratio total height/d.b.h., it is necessary to know if this is true for western redcedar. If so d.b.h. and height can be manipulated independently.

Table 5.--Correlation among plot variables for conebearing stands, 11 degrees of freedom

	2-tree mean d.b.h.	2-tree mean d.b.h./ height	plot mean d.b.h.	cedar mean d.b.h.	plot basal area	cedar basal area	total stems/ acre	cedar stems/ acre
2-tree mean height	0.694 **	0.485 n.s.	0.375 n.s.	0.526 n.s.	0.239 n.s.	0.261 n.s.	-0.376 n.s.	-0.356 n.s.
2-tree mean d.b.h.		-0.282 n.s.	0.702 **	0.825 **	0.587 *	0.623 *	-0.554 *	-0.301 n.s.
2-tree mean height/d.b.h.			-0.378 n.s.	-0.317 n.s.	-0.341 n.s.	-0.362 n.s.	0.200 n.s.	-0.059 n.s.
plot mean				0.829 **	0.784 **	0.314 n.s.	-0.866 **	-0.596 *
cedar mean d.b.h.					0.526 n.s.	0.454 n.s.	-0.860 **	-0.627 *
plot basal area						0.528 n.s.	-0.450 n.s.	-0.240 n.s.
cedar basal area							-0.027 n.s.	0.330 n.s.
total stems/acre								0.852 **

* Indicates the correlation was significant at P<5%.
** Indicates the correlation was significant at P<1%.
n.s. Indicates the correlation was not significant at P<5%.

Table 6.--Relative amounts of phenotypic variation in ratio of total height to d.b.h. by conebearing status

	Among-stand variation as % of total phenotypic variation	Within-stand variation as % of total phenotypic variation
Nonbearing stands	85.4	14.6
Conebearing stands	75.6	24.4

The correlation of total number of stems and number of cedar stems with the ratio total height/d.b.h. in nonbearing stands may indicate an environmental effect of stand dynamics on that ratio. The lack of such correlation in conebearing stands suggests that the number of stems cannot explain all the variation in that ratio. More information is needed to separate the environmental factors out of the height to d.b.h. ratio.

Western redcedar conebearing in closed stands in Idaho is not as common, especially in a dry year, as it may be in coastal forests. This variability in cone production may mean that vegetative propagation of materials obtained from ortets in natural stands is a better way of sampling genetic variation than collecting cones. If it is desired to sample genetic variation by collecting cones, it may be useful to be able to discriminate between stands that will be likely to be bearing cones and those that will not. The sample size used in the present research was not large enough to permit development of a predictive model. Use of the means reported here, however, may permit a reduction in time and travel required in locating stands bearing western redcedar cones. Further research on conebearing status of western redcedar stands would increase the sample size and permit estimation of differences between years. It might also permit development of a predictive model which would reduce the time and travel involved in finding natural western redcedar stands which are bearing cones.

If there are wet-site-adapted and dry-site-adapted genotypes of western redcedar this knowledge could be utilized in reforestation efforts. Perhaps it would be economical to plant western redcedar on drier sites than where it is climax. However, the present research cannot answer whether there are dry-site-adapted and wet-site-adapted genotypes of

western redcedar. Further research using replicated field plantations of progenies from trees on both kinds of site could be used to estimate genetic and environmental components of the difference between cedar producing cones on moist sites and cedar not producing cones on dry sites. Chemical and biochemical estimates of variability might also provide estimates of genotypic and environmental effects.

The outstanding characteristic of western redcedar is its conical shape (Anderson 1961). While a conical shope may be ideal for utility poles, it may not be the best stem form for other products. If the stem form of western redcedar could be improved, the yield of other products such as lumber might be improved. Estimates of the effect of environmental factors on the height-to-diameter ratio can be made by further research in natural stands. A possible association with age or buttressing should be investigated, and the effect of slope position and elevation should be tested. The present research has shown that number of stems per hectare and number of cedar stems per hectare were correlated with the height-to-diameter ratio in nonbearing but not in conebearing stands.

To estimate the extent to which breeding progress can be made in changing the height-to-diameter ratio, replicated plantations should be established containing progenies of trees from a number of stands. The number of trees per stand whose progenies are represented should be fairly high.

Knowledge of the site requirements for western redcedar cone production and of climatic factors affecting cone production may permit seed orchard establishment on sites where seed production can be maximized and outside pollen can be minimized. Some research needs to be done to clarify whether western redcedar seed orchards can be established on a dry site, so that irrigation can supply necessary soil moisture during each month and the seed orchard can be established some distance away from sources of western redcedar pollen. In some species, a slight drought at or before the period of cone initiation promotes the induction of large numbers of cones. Research is needed to test the effect of a slight drought on western redcedar cone initiation. Results of the present research provide some information which has a bearing on western redcedar seed orchard management and cone production. The possibility of pollen desiccation and conditions under which it may occur should also be investigated.

Research on phenology of western redcedar flower induction, flowering, and pollination in Idaho is needed to at least partially explain the results obtained in the present research, to indicate which months and what kind of weather are critical and as preparation in case any controlled pollination experiments in an outdoor breeding arboretum need to be done.

CONCLUSIONS

It was not possible in the present research to separate environmental effects from genetic ones. The objective of the present research was to obtain preliminary information about variation in and among natural western redcedar (*Thuja plicata* Donn.) stands, including information about the reproductive biology of western redcedar in Idaho.

Twenty-six stands were selected having an average composition of approximately 50 percent cedar by number of stems or by basal area and a mean d.b.h. of approximately 12 inches (30 cm). Half the stands were bearing western redcedar cones; all but one were bearing the previous year cones. In general, stands selected had closed canopies and no standing water on the site.

The ratio of total height to d.b.h. of two dominant or codominant cedars did not differ significantly between the two kinds of stands. The ratio of total height/d.b.h. was significantly correlated with number of stems/ha and with number of cedar stems/ha in nonbearing stands indicating a possible stand influence. Total height of two dominant or codominant cedars had a correlation of 0.858 with d.b.h. of the same trees in nonbearing stands, but only 0.694 in conebearing stands. Both correlations were significant at the 1 percent level. These correlations, being different, suggest a possibility of d.b.h. and height having a degree of independence.

Conebearing stands had a mean elevation of 1125 m. Conebearing stands had higher basal areas of grand fir and/or western hemlock. Reproduction in conebearing stands was more likely to be a combination of grand fir, western hemlock, and cedar.

Conebearing stands tended to be on high-elevation, moist sites, and nonbearing stands tended to be on drier sites at lower elevation. There is some variation in the total height to d.b.h. ratio. More research will be needed to estimate environmental and genetic components of the variation in ratio of total height to d.b.h. and to estimate environmental and genetic components of the differences between conebearing and nonbearing stands, particularly with regard to the difference between stands bearing cones on moist sites and stands not bearing cones on drier sites. Improvement in the conical shape of cedar is a potential. If there are dry-site-adapted genotypes of cedar, they could be utilized on a wider range of sites than those on which cedar is climax. However the present research is not able to separate environmental effects from genetic ones, which is information needed to determine any wet-site or dry-site adaptations.

ACKNOWLEDGMENT

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EFFECTS OF COLD STRATIFICATION AND SEED COAT STERILIZATION TREATMENTS ON PINYON (PINUS EDULIS) GERMINATION

Gerald J. Gottfried and L. J. Heidmann

ABSTRACT: One experiment compared germination capacity and energy of pinyon (Pinus edulis Engelm.) after 30- and 60-day cold stratification. Seed from five Arizona seed sources were compared. Both treatments did not affect germination capacity, but increased speed of germination. A second study evaluated the effects of six hydrogen peroxide treatments designed to improve germination and suppress mold growth during prolonged tests. Results were variable. Except for one seedlot, treatment did not improve germination capacity or energy, nor did it suppress mold. The most concentrated treatment tended to suppress germination.

INTRODUCTION

Pinyon-juniper woodlands occupy approximately 13.4 million hectares (33 million acres) in the southwestern United States. The type covers 17 percent of Arizona, mostly in the northern half, and 26 percent of New Mexico (West and others 1975) where it occurs statewide, except in the southeastern and south-central areas (Springfield 1976). The woodlands consist of pinyon (Pinus edulis Engelm.) and one or more of the following junipers: Utah juniper (Juniperus osteosperma (Torr.) Little); one-seed juniper (J. monosperma (Engelm.) Sarg.); alligator juniper (J. deppeana Steud.), and Rocky Mountain juniper (J. scopulorum Sarg.). The type is found between 1 371 and 2 438 m (4,500 and 8,000 ft) elevation; precipitation can vary from 300 to 550 mm (12 to 22 inches). It grows on a wide variety of soils and parent materials (Springfield 1976).

Management objectives for pinyon-juniper woodlands in the Southwest appear to have recently shifted towards more intensive production of wood products. Better knowledge of woodland ecology is needed to develop suitable forestry practices for these areas. Information is needed about the germination requirements of pinyon and junipers with respect to climatic factors, such as light and moisture, and physiological factors, such as seed dormancy.

The current studies concentrate on dormancy in pinyon seed. This species is of particular interest because it occurs throughout the woodland zone, and is economically important for fuelwood, especially in New Mexico, and for edible nuts. Little is known about seed dormancy of pinyon under natural conditions, or how storage will affect dormancy. Some pine species show little evidence of dormancy, while in others, up to 3 years may elapse before germination occurs (Krugman and Jenkinson 1974). Cold stratification is a common technique for breaking embryo dormancy, but its application to pinyon is poorly documented according to Krugman and Jenkinson (1974).

Understanding seed dormancy is important in research involving the effects of various environmental factors on pinyon germination and establishment. This knowledge is critical to successful growth of planting stock or for regeneration by artificial seeding. Sowing untreated seed during dormancy would lengthen the germination period, and expose seed to adverse conditions for longer periods. Seed from different locations might exhibit different degrees of dormancy and might respond differently to stratification treatments.

To solve the problem of mold in long-term germination studies, Riffle and Springfield (1968) used a 30-minute soak with 30-percent hydrogen peroxide alone, or in combination with a water soak or wash, to prevent the development of seedborne fungi. They also found that pinyon seed treated with peroxide, alone or in combination with water, germinated twice as fast as untreated seed during the first 8 days of a 28-day test period. According to Kramer and Kozlowski (1979), hydrogen peroxide stimulates seed respiration, which is essential for the early phases of germination.

The two studies reported here were designed to evaluate the effects of cold stratification and various hydrogen peroxide treatments on pinyon germination capacity and germination energy. Germination capacity is the percent of filled seeds which germinate during a period of time ending when germination is essentially complete. Germination energy is defined as the number of days necessary to achieve 50 percent germination of filled seeds. The hydrogen peroxide treatments also were evaluated for their ability to suppress mold contamination of seed during testing.

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METHODS

Seed Sources

Pinyon seed was collected from five locations in central Arizona (fig. 1). Trees from the Prescott area contained both 1- and 2-needle fascicles, and have been classified as either P. edulis var. fallax or as a P. edulis x P. monophylla hybrid (Lanner 1974). Seed from Deadman Flat was collected in 1979, and from the other sources in the fall of 1983. The seed was stored at 3° C (37° F). Site characteristics of the collection areas are given in table 1; elevations were taken from U.S. Geological Survey topographic maps. Mean annual precipitation values are for the nearest weather station (Sellers and others 1985), except for Cedar Ranch, which is not near any station.

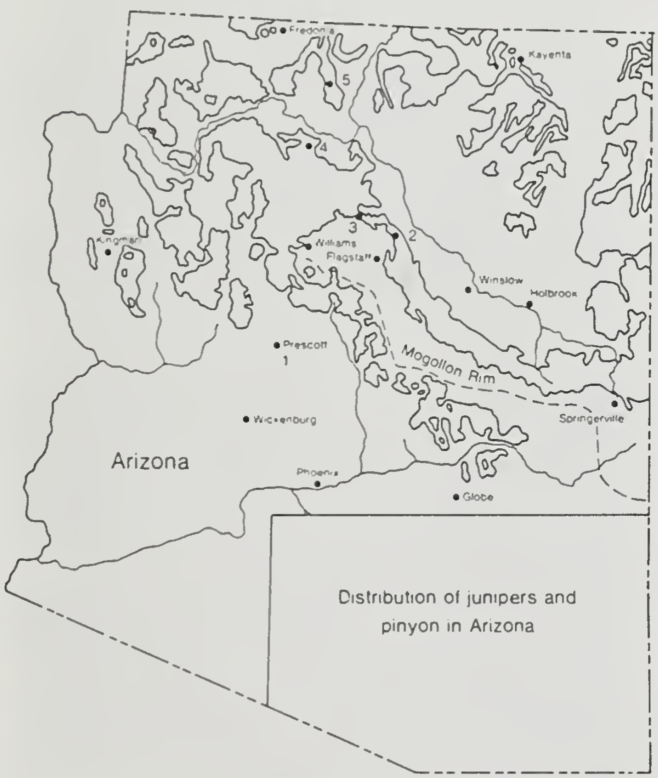

Figure 1.--Map of the pinyon-juniper woodlands in Arizona (Arnold and others 1964) and the location of the seedlots: (1) Prescott, (2) Deadman Flat, (3) Cedar Ranch, (4) Tusayan, and (5) North Kaibab.

Table 1.--Characteristics of the five pinyon provenances

Location	Elevation	Pinyon height in stand	Mean annual precipitation
	- - meters	- -	mm
Prescott	1,689	7.3	480
Deadman Flat	2,054	4.8	408
Cedar Ranch	2,195	12.7	--
Tusayan	2,091	15.1	385
N. Kaibab	2,073	10.6	508

Cold Stratification Experiment

The experiment compared 30- and 60-day cold-stratification treatments with a control treatment. Seeds from each seedlot were rinsed in distilled water, then were wrapped in moistened paper towels. Wrapped seeds were put into a double plastic bag, loosely sealed, and placed in a refrigerator at 3° C (37° F). Towelling for the 60-day treatment was changed after the first 30 days. The first lot was started in March and the second in April 1984.

After stratification, 25 seeds from each of the three treatments in each seedlot were placed on glass-fiber filter paper in 10-centimeter disposable petri dishes. There were five subsamples of each seedlot-treatment combination, for a total of 75 dishes. Dishes were randomized on each of five shelves, which contained one subsample. Seeds were germinated in a Hoffman germinator programmed for 12 hours of light at 23.9° C (75° F) and 12 hours of dark at 20° C (68° F). Daytime temperature was 6.1° C (11° F), lower than recommended by the International Seed Testing Association (Krugman and Jenkinson 1974); however, preliminary tests indicated better germination at 23.9° C (75° F) than at 30° C (86° F). Although Krugman and Jenkinson (1974) recommended a schedule of 8 hours of light and 16 hours of darkness, the 12-hour interval was used, because it may better approximate conditions during the germination period, which was assumed to be summer. However, it is not known whether P. edulis germinates in the spring, summer, or during both seasons under natural conditions. The trials were not replicated in different germinators or for other time periods.

Dishes were monitored daily and were watered as necessary. Germination was recorded when the radicle equaled the length of the seed. Germinated seeds were discarded. Counts were made for 33 days until germination had essentially ended. Ungerminated seeds were cut open to determine if they were filled.

Hydrogen Peroxide Experiment

The hydrogen peroxide trial consisted of seven treatments as follows:

Treatment Number	Treatment Description	
1	Control	
2	3% H_2O_2	2½-minute soak
3		5-minute soak
4		10-minute soak
5	30% H_2O_2	2½-minute soak
6		5-minute soak
7		10-minute soak

Seeds were stirred continuously during the soaking period. Four seedlots were treated; seed from Deadman Flat was not included because of insufficient seed. Five subsamples were set up for each treatment combination. Twenty-five seeds were placed on glass-fiber filter paper in each 10-centimeter petri dish; there were 140 dishes with 28 dishes on each of five shelves. The experiment was started in January 1985.

The same germination and counting procedures used in the stratification study were followed. Counts were made for an average of 44 days. Shelf order in the germinator was rotated to avoid possible germination differences caused by microclimatic variations in the equipment. In addition, the day when mold first appeared in a dish was noted. Experience indicates that most seed becomes contaminated soon after mold is first detected.

Treatment differences in both studies were compared by one-way analysis of variance using pooled seed source as a blocking factor. Pairwise differences were calculated using Fisher's F-protected least significant difference test. One-way analysis of variance procedures were used to test for treatment differences within seedlots, and Duncan's multiple-range test was used to isolate any differences. Significance was indicated by P values at or below the 5 percent level. Germination capacity was analyzed after arc sin transformation of these data to improve variance homogeneity. Although there appeared to be differences among seedlots, they could not be evaluated statistically, because by combining the seed, spatial variability within each seed source area could not be determined. All analyses within seedlots are based on estimates of subsampling variability, not spatial variability within a seed source. A t-test was used to compare germination differences within control treatments over time.

RESULTS

Cold Stratification

Germination capacity.--The germination capacity of filled seeds was not significantly different among treatments. The averages, with standard deviations, ranged from 92.26 ± 0.05 percent for the control to 88.20 ± 0.08 percent for 30-day stratification. The range among seedlots was also small (14 percent), varying from 98 percent on the North Kaibab to 84 percent at Deadman Flat.

Germination energy.--There were differences between treatments in the number of days to reach 50 percent germination, with germination significantly faster for cold stratification treatments than for the control (table 2). Seed from the Prescott and North Kaibab showed the greatest response to cold stratification, with 50 and 82 percent decreases, respectively, in time necessary for 50 percent germination. Sixty days of cold stratification produced more rapid germination than the 30-day treatment or the control for Deadman Flat, Cedar Ranch, and Tusayan seed. However, combining the data for the five seedlots tended to reduce the difference between stratification treatments, although both were still different than the control.

The control treatments.--There appeared to be no differences in germination capacity among seedlots. Differences were apparent in germination energy. The Cedar Ranch and North Kaibab seed germinated in an average of 10.6 days, while the other three seedlots germinated in an average of 17.1 days.

Hydrogen Peroxide Treatments

Germination capacity.--Analysis of the hydrogen peroxide treatments indicated differences for the pooled seedlots (table 3). Seeds receiving the 30-percent hydrogen peroxide soak for 10 minutes germinated least (52.4 ± 25.3 percent), and significantly less than seed receiving the 3-percent solution for 5 or 10 minutes or the 30-percent solution for 2.5 minutes. These three treatments averaged 83.3 percent. The 30-percent solution for 10 minutes was similar to the control, the 3-percent for 2.5 minutes, and the 30-percent for 5-minute treatments.

Some treatment differences also were noted within three of the four seedlots (table 3). Only seeds from Cedar Ranch showed no significant differences among treatments. Germination percentages for seeds receiving the 30-percent hydrogen peroxide soak for 10 minutes were consistently lower than any other treatment within seedlots. Even the Cedar Ranch ecotype showed a slight drop of 10 percent in germination compared to the control. A drop in germination of 38 percent was noted for North Kaibab seed. The Tusayan control did not germinate well; however, the difference between the 30-percent peroxide for 10-minute treatment and the best Tusayan germination (30-percent peroxide for 2.5 minutes), which was helped by treatment, was about 46 percent.

Two of the seedlots also showed significant germination differences for the 30-percent

Table 2.--Germination energy expressed as the average number of days (with standard deviation) to achieve 50-percent germination of filled seed after cold stratification

Seedlot treatment	Prescott	Deadman Flat	Cedar Ranch	Tusayan	N. Kaibab	Total
Control	16.2±2.8 a[1]	17.6±1.5 a	10.2±0.8 a	17.6±0.9 a	11.0±0.7 a	14.5±3.6 a
30-day stratification	8.2±3.0 b	11.6±2.4 b	6.2±0.8 b	12.0±1.6 b	1.8±0.4 b	8.0±4.2 b
60-day stratification	5.6±2.1 b	9.6±0.9 c	4.4±1.1 c	8.4±2.7 c	1.8±0.4 b	6.0±3.1 b

[1]Means within each column followed by different letters are significantly different at the 5 percent level.

Table 3.--Average germination capacity (percent with standard deviation) for filled seed after hydrogen peroxide treatment

	Prescott	Cedar Ranch	Tusayan	N. Kaibab	Combined
Control	83.5± 3.7 bc[1]	94.4± 3.6 a	26.7±14.3 a	85.0± 3.9 c	72.4±30.8 ab
3% x 2.5 min	87.5±10.4 c	90.3± 3.7 a	30.3±11.7 a	89.9± 6.4 c	74.5±29.5 ab
3% x 5 min	88.7± 6.7 c	90.4±10.4 a	65.1± 9.6 b	87.9± 6.3 c	83.0±12.0 b
3% x 10 min	87.5± 3.3 c	92.8± 6.6 a	61.6±17.6 b	86.3± 5.4 c	82.0±13.9 b
30% x 2.5 min	83.5± 6.8 c	94.4± 3.6 a	69.6± 8.3 b	91.9± 3.0 c	84.8±11.2 b
30% x 5 min	69.2±16.7 ab	94.4± 4.5 a	64.8±10.4 b	70.8± 7.6 b	74.8±13.3 ab
30% x 10 min	54.2±15.2 a	84.7±10.6 a	23.2± 8.2 a	47.4±16.7 a	52.4±25.3 a

[1]Means within each column followed by different letters are significantly different at the 5 percent level.

5-minute treatment (table 3). This treatment for Prescott (69 percent germination) was statistically similar to the control and to the 30-percent 10-minute soak but less than for the other treatments, which averaged 87 percent. The 30-percent 5-minute soak for North Kaibab (71 percent) was higher than the 10-minute soak in 30-percent peroxide (47 percent) but lower than the other five treatments, which averaged 88 percent. However, the 30-percent 5-minute treatment produced relatively good germination at Tusayan.

Comparing data from the controls of the stratification and the peroxide tests indicated that Tusayan germination capacity decreased from May 1984 to January 1985. The control averaged 87 percent germination for the cold stratification test, and 27 percent for the hydrogen peroxide test. A comparison of control germination capacities for the other seedlots also showed decreased germination:

	1984	1985
Prescott	87.8	83.5
Cedar Ranch	97.5	94.4
North Kaibab	97.4	85.0

T-tests, however, indicated that only the North Kaibab seed germination capacity had also dropped significantly over the 8 months.

Germination energy.--The analysis of variance for the combined data also indicated significant differences among treatments (table 4); but the differences between treatments could not be demonstrated by the Fisher's F-protected test. It appears that seeds which received the 30-percent 10-minute soak took longer to reach 50 percent germination than it took seeds receiving the other treatments.

Comparisons within seedlots generally indicated that the 30-percent 10-minute treatments retarded germination energy, while the other treatments had no effect. Tusayan was an exception, however, exhibiting the same trend as germination capacity. The control group did very poorly, while some peroxide treatments stimulated germination. The control group never achieved 50 percent germination.

Mold.--The various peroxide treatments did not prevent or delay the contamination of seed by various seed or airborne fungi. The only significant delay--about 7 days compared to the control--was for the 30-percent 5-minute treatment of Prescott seed. There also appeared to be differences among seedlots. Cedar Ranch seed became contaminated after 23 days, while Prescott seed became contaminated in 4 days. Contamination was noted on the Prescott seed during the stratification period in the first trial. Tusayan and North Kaibab were contaminated within 10 days.

Table 4.--Germination energy expressed as the average number of days (with standard deviation) to achieve 50-percent germination of filled seed after hydrogen peroxide treatment

	Prescott	Cedar Ranch	Tusayan	N. Kaibab	Combined
Control	12.8± 1.1 a[1]	10.2±0.2 a	44.4± 2.2 a	10.2± 0.8 a	19.4±16.7 a
3% x 2.5 min	12.2± 0.4 a	10.2±0.2 a	44.4± 2.2 a	10.4± 0.5 a	19.3±16.8 a
3% x 5 min	12.0± 0.7 a	10.4±0.2 a	24.4± 5.5 b	11.2± 1.1 a	14.5± 6.6 a
3% x 10 min	12.0± 1.2 a	10.2±0.2 a	31.6±11.7 b	11.4± 1.3 a	16.3±10.2 a
30% x 2.5 min	12.4± 1.5 a	10.4±0.2 a	26.4± 5.1 b	11.0± 0.7 a	15.0± 7.6 a
30% x 5 min	20.6±15.4 a	10.4±0.2 a	29.0± 5.7 b	14.2± 3.0 a	19.3± 8.1 a
30% x 10 min	33.0±17.0 b	11.6±0.4 b	44.4± 2.2 a	31.2±14.1 b	30.0±13.6 a

[1]Number within a column followed by the same letter is not significantly different at the 5 percent level.

A sample of contaminated seeds was inspected by Dr. J. States, Biology Department, Northern Arizona University. He identified: Penicillium (2 species), yeast (3 species), Alternaria, Cladosporium, Bispora, Gliocladium, and Rhizopus. Dr. States indicates that the molds will attack and kill germinating seedlings under high moisture conditions. No effort was made to relate genera to specific hydrogen peroxide treatments.

DISCUSSION AND CONCLUSIONS

Cold Stratification

Although the germination capacity of filled seeds was not significantly different among treatments, cold stratification affected the germination energy of pinyon. Both the 30-day and 60-day treatments germinated faster than the control. Some seedlots did better after 60 days than after 30 days. Results over all seedlots, however, indicated no differences between stratification periods. While it is difficult to make recommendations after testing five seedlots, the more rapid germination of pinyon seed after cold stratification was consistent. It appears that a 30-day treatment should be sufficient for laboratory or greenhouse purposes where ideal environmental conditions are uniformly maintained. A 60-day stratification period may be more beneficial for field sowing because suboptimal conditions often occur. For example, Allen (1960) found more rapid germination of Douglas-fir (Pseudotsuga menziesii Mirb. Franco) seed following long stratification periods of up to 150 days when spring temperatures were low. Local seed should be tested to evaluate the effects of cold stratification, especially if large seeding operations are being considered.

A comparison of germination energy for the control treatments suggested differences among seedlots. The Cedar Ranch and North Kaibab seed germinated in an average of 10.6 days, 6.5 days earlier than the average for the other three seedlots.

Some combination of elevation and latitude may be responsible for the difference between the two groups. Either factor alone did not seem to influence this difference, because Cedar Ranch is south of Tusayan, while Tusayan and Deadman Flat are at a similar elevation as the North Kaibab. The growing season most likely starts later, and is shorter on more northern sites or above 2 134 m (7,000 ft). The ability to germinate quickly once proper climatic conditions are reached would give higher elevation or northern seedlings more time to become established before the onset of severe conditions, especially drought.

Hydrogen Peroxide Treatments

Although most treatments did not affect germination capacity, relative to the controls (table 3), germination capacity generally appeared lowest for seed receiving the 30-percent 10-minute treatment. Riffle and Springfield (1968), working with pinyon seed from Santa Fe, New Mexico, found that a 30-minute soak with 30-percent hydrogen peroxide treatment produced a slight but nonsignificant 18-percent increase in germination. They reported that combining water treatments with the hydrogen peroxide treatment improved germination relative to their control; but the results from all hydrogen peroxide treatments were similar.

Germination energy was generally depressed, or in the case of Tusayan, not improved by the 30-percent 10-minute treatment (table 4). Riffle and Springfield (1968), in contrast, indicated that all of their hydrogen peroxide treatments improved germination.

Ecotypic variability could account for the different results encountered in the seedlots, and for the differences with Riffle and Springfield (1968). They only tested one seed source and recognized the fact that other seedlots could react differently. The conclusions from this study also would have been different if the tests had been conducted on either Cedar Ranch or Tusayan seed alone.

Ecotypic differences also may have been a factor causing the decrease in germination capacity of the two northern seedlots (Tusayan and North Kaibab) while in storage. All attempts were made to handle all seed similarly. Meeuwig and Bassett (1983) reported that pinyon seed lost viability rapidly after 1 year; however, this may be under natural conditions. Other investigators indicated difficulties maintaining viability of singleleaf pinyon (P. monophylla) seeds under storage (Budy 1985). However, the Deadman Flat seed used in the stratification test had a germination capacity of 84 percent after 4½ years in storage. This seed was stored in a closed glass jar, while the 1983 seeds were stored in paper bags placed in loosely closed plastic bags. While this may account for better germination of Deadman Flat seed, it does not explain the differences with Cedar Ranch or Prescott seed.

The six hydrogen peroxide treatments did not prevent or delay contamination of seed by mold. Riffle and Springfield (1968) found that their treatments prevented contamination. Differences in techniques, and the longer period of treatment, may account for the different results. Dishes in this study could have been recontaminated by airborne spores. However, the hydrogen peroxide did not reduce the growth of seed fungi initially present or of new contamination by airborne fungi. Riffle and Springfield (1968) also identified Penicillium, Alternaria, and Rhozopus plus Trichoderma, Cephalosporium, Aspergillus, and Fusarium. Differences in the number of days before contamination was noted and varied by seedlot, again indicating possible ecotypic variation.

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ACETONE IS UNRELIABLE AS A SOLVENT FOR INTRODUCING GROWTH REGULATORS INTO SEEDS OF SOUTHWESTERN PONDEROSA PINE (PINUS PONDEROSA VAR. SCOPULORUM)

L. J. Heidmann

ABSTRACT: Acetone is reported to be a reliable solvent for introducing plant growth regulators into various seeds without affecting germination. Several experiments in which southwestern ponderosa pine seeds were soaked in acetone for periods of 1 to 24 hours, then germinated under various temperature regimes, gave negative results even at soaking periods as short as 1 hour. Acetone is not an appropriate solvent for introducing plant growth regulators into southwestern ponderosa pine seeds.

INTRODUCTION

Germination of southwestern ponderosa pine (Pinus ponderosa var. scopulorum) is temperature-dependent (Pearson 1950; Larson 1961). Under ideal temperatures in the laboratory, 20° to 25° C (68° to 77° F), 50 percent of seeds germinate in a few days (Heidmann 1981). In the field, during the germination period, diurnal fluctuations in temperature of 4.4° to 26.7° C (40° to 88° F) are common. Under these conditions, germination may take several weeks. Cytokinin and abscisic acid (ABA) levels appear to be related to temperature changes. An increase in the level of ABA and a decrease in cytokinin have been shown during temperature stress, and are correlated with a reduction in shoot growth (Itai and others 1973). Lettuce seeds, in the dark at 35° C (95° F), were not released from dormancy by kinetin or gibberellic acid (GA_3); however, when GA_3 was supplied with kinetin, germination occurred (Khan 1975).

Dormancy in plants and seeds is likely under the control of naturally occurring hormones. According to Khan (1975), gibberellins (GAs), inhibitors such as ABA, and cytokinins have primary, preventive, and permissive roles in control of seed germination. Gibberellic acid will promote germination in the absence of ABA; but when ABA is present, GA_3 will only promote germination in the presence of cytokinin.

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Heidmann (1981) showed that GA_3 and several other compounds significantly reduced the time required for 50 percent germination of southwestern ponderosa pine seeds under fluctuating temperatures similar to those encountered in the field. The compounds were applied as an aerated soak. Aeration in water alone significantly reduced the time to 50 percent germination, presumably because of the effect of oxygen. Although stimulation of germination by oxygen is a desirable trait, it masks the effect of the compounds being studied. Therefore, to eliminate the confounding effect of oxygen and to isolate the effect of the growth regulators under study, another method of introducing regulators into the seeds is required.

Tao and Khan (1974) showed that GA_3 and indole-3-acetic acid (IAA) can be introduced into the embryos of various dry seeds with acetone. Acetone itself did not adversely affect germination.

In 1983 and 1984, a series of experiments was conducted to determine the effect of acetone on the germination of southwestern ponderosa pine seeds. If acetone did not modify germination patterns, then it was to be used to introduce GA_3, ABA and N-6-benzyladenine (a cytokinin), singly or in combination, into pine seeds.

METHODS

Four experiments were conducted. The first three experiments were conducted in a similar manner. Seeds were collected on the Coconino National Forest, approximately 40 km (25 mi) north of Flagstaff, AZ, at an elevation of about 2 440 m (8,000 ft). Seeds were collected in 1979 and were stored at -17° C (2° F) until use. Viability in 1980 was 98 percent. Seeds were soaked in 100 ml of acetone for 0, 4, 8, 16, and 24 hours. After soaking, seeds were rinsed several times in distilled water, then were placed on Whatman glass fibre filter paper in 10-cm (3.9-inch) disposable petri dishes. International Seed Testing Association guidelines (1976) suggest using four replications of 100 seed for conducting germination experiments. However, because of a scarcity of seed, six replications of 50 seeds were used in the first three experiments, and five replications were used in the fourth. Treatments were randomized within replications, then dishes were placed on a single shelf in a Hoffman seed germinator set, for 16-hour days and 8-hour nights. In experiment 1, day temperature was

maintained at 27° C (80° F) and night temperature at 7° C (45° F). For experiment 2, temperatures were 24° C (75° F) for days and 4.4° C (40° F) for nights. Temperatures for experiment 3 were 24° C (75° F) days and 18° C (65° F) nights. Temperatures chosen were those likely to be used in conducting germination tests with plant growth regulators. Results from tests conducted at optimum temperatures were compared to those from experiments using temperatures similar to those encountered in the field during the germination period.

Dishes were watered as necessary with distilled water. Care was taken not to overwater, because germination percentages of southwestern ponderosa pine seeds are lowered considerably by excess water (Rietveld 1985). Germination counts were made daily. Seeds with a radicle of 5 mm (0.2 inch) in length were recorded as germinated, then were discarded.

Experiment 4 was conducted with seeds collected on the North Kaibab Ranger District of the Kaibab National Forest, in 1962, at an elevation of approximately 2 440 m (8,000 ft). Viability of the seed was 90 percent in 1980. The experiment was conducted in the same manner as the first three experiments, except that seeds were soaked in acetone for 0, 1, 2, and 3 hours. For this experiment, a Percival germinator was used. Day length was 16 hours at 24° C (75° F), and night length was 8 hours at 18° C (65° F).

Treatment means for all experiments were analyzed using Dunnett's T3 multiple comparison procedures for heterogeneous variance (P=0.10). Individual T-tests between treatments were also run (P=0.01 and 0.05).

RESULTS AND CONCLUSIONS

Results from the four experiments were inconsistent with wide variability. In the first three experiments, soaks in acetone of 8 hours or more generally reduced germination (table 1, P=0.1). In experiments 1 and 3, a 24-hour soak almost completely repressed germination; in the second experiment, this treatment was not significantly different from the control. Although a 4-hour soak is not significantly lower than controls, the germination is as much as 30 percent less (table 1).

Responses to germination temperatures were equally unpredictable. The first two experiments utilized minimum temperatures likely to be encountered in the field during the summer germination period. A temperature regime of 27° C (80° F) days and 7° C (45° F) nights, resulted in the highest germination percentage for the control (84 percent), while germination for the 24-hour soak was only 4 percent. Dropping the maximum and minimum temperatures 2.8° C (5° F) reduced control germination 22 percent, but resulted in a 40 percent increase in germination for seeds soaked 24 hours. In the third experiment, conducted under what are considered optimum temperatures, there was virtually no germination for the 16- and 24-hour soaking periods.

Information from the first three experiments seemed to indicate that a shorter soaking time might be desirable. This is refuted by results from experiment 4 which show that a 1-hour soak significantly reduced germination. Individual T-tests between the control and the other three treatments showed that each of the soak treatments

Table 1.--Effect of various acetone treatments on germination of southwestern ponderosa pine seeds

Soak Time (hours)	Experiment Number 1: Germ[1] %	1: Std. Dev.	2: Germ[1] %	2: Std. Dev.	3: Germ[1] %	3: Std. Dev.	4: Soak Time (hours)	4: Germ[4] %	4: Std. Dev.
0	84.33a[2] a[3]	7.53	62.00a[2] a[3]	15.65	79.67a[2] a[3]	4.46	0	77.60a[2] a[3]	3.85
4	69.67a ab	27.75	58.00a a	9.63	48.33a a	25.91	1	46.80b b	20.62
8	21.00b bc	23.58	14.33c b	12.42	8.67b b	5.89	2	52.40a b	22.60
16	14.67b c	15.68	19.33bc b	23.55	0.00c c	0.00	3	39.60a b	31.09
24	4.00b c	6.20	44.33ab a	5.57	0.33c c	0.82			

[1]Mean of 6 replications of 50 seeds.

[2]Means within each column followed by the same letter are not statistically different at the 0.1 level according to Dunnett's T3 multiple comparison procedure.

[3]Means within each column followed by the same letter are not statistically different at the 0.01 level for experiments 1, 2, and 3 or at the 0.05 level for experiment 4 according to individual T-tests between pairs of treatments.

[4]Mean of 5 replications of 50 seeds.

reduced germination significantly (P=0.05). The discrepancy between Dunnett's multiple comparison procedure and individual T-tests is because Dunnett's method is based on an overall experiment-wise Type I error, and individual T-tests use a comparison-wise Type I error (King 1985).

These results confirm the erratic behavior of southwestern ponderosa pine seeds when treated with various materials. Although seeds can be treated with strong oxidizing agents, such as hydrogen peroxide, without affecting germination (Heidmann 1981), other treatments, such as a 15-second soak in sodium hypochlorite (Clorox), significantly repressed germination (Ronco 1985). It appears that acetone adversely affects the germination of ponderosa pine seeds. Soaking periods as short as 1 hour significantly repressed germination. This is contrary to findings by Tao and Khan (1974) that indicate various seeds can be soaked in acetone for as long as 28 hours without affecting germination. Milborrow (1963) soaked several species of seeds in acetone for periods as long as 3 months without deleterious effects. The primary conclusion to be drawn from these experiments is that acetone is unreliable as a solvent for introducing materials into the embryos of ponderosa pine seeds. In experiments currently in progress, growth regulators are being introduced to the embryos under vacuum.

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ARE YOU GETTING PONDEROSA PINE AND DOUGLAS-FIR CONE CROPS AT HIGH ELEVATIONS?

Glenn L. Jacobsen

ABSTRACT: Research documentation and personal observations of cone crops at the upper elevation ranges of old-growth ponderosa pine and Douglas-fir in Central Idaho indicate a longer cone crop interval than the normal interval of 4 to 5 years for ponderosa pine. It appears that cone crops for ponderosa pine at 5,500- to 6,000-foot elevations and Douglas-fir at 6,000- to 6,500-foot elevations must coincide with a heavy to extremely heavy cone crop at lower elevations before we can obtain a collectible cone crop.

INTRODUCTION

Review of research literature for the Idaho area, Lucky Peak Nursery reports from 1965 to 1984, and observations made on the Payette and Boise National Forests in Central Idaho indicate a wide range of variability of cone crops, especially with ponderosa pine and Douglas-fir.

In Central Idaho, ponderosa pine on commercial forest land occurs between the elevations of 3,000 to 6,500 feet above sea level. Douglas-fir occurs between the elevations of 3,500 to 7,000 feet. The vast majority of these species are in old growth stands that are in a static condition. Cone crop records generally indicate the lower the elevation the heavier the cone crop. Cone crops of ponderosa pine at the 5,500- to 6,000-foot elevation and Douglas-fir at the 6,000- to 6,500-foot elevation have been very sparse.

The trend appears to be that whenever conditions are right for a better than average ponderosa pine cone crop, we also have at least an average Douglas-fir cone crop. This may vary by Ranger District and areas within Districts.

RESEARCH

Heavy ponderosa pine crops were documented (Curtis and Foiles 1961) in Central Idaho in the following years:

- 1936 - Heavy cone crop
- 1940 - Heavy cone crop
- 1941 - Cool moist summer--widespread establishment of seedlings
- 1958 - Extremely heavy cone crop
- 1959 - Below normal summer rainfall--poor establishment of seedlings
- 1962 - Average crop - less than 1/2 size of 1958 crop
- 1963 - Cool, moist summer months--unusually successful natural regeneration

No research data are available on cone crops from 1964 to the present time for Central Idaho.

CONE COLLECTION RECORDS

Cone collection records for the Payette National Forest indicate collectible cone crops in the following years, although most crops were light. Heavy ponderosa pine crops occurred in 1958, 1962, and 1971. Collectible crops are defined as one bushel of cones per tree.

Year	Species	Elevation range (feet)
1958	Ponderosa pine	Unknown
1962	Ponderosa pine	3,000 - 4,000
1963	Ponderosa pine	3,000 - 4,000
1964	Ponderosa pine	3,000 - 5,000
	Douglas-fir	4,000 - 6,000
1965	Ponderosa pine	3,000 - 4,000
	Douglas-fir	4,000 - 5,000
1971	Ponderosa pine	4,000 - 6,000
	Douglas-fir	5,000 - 6,000
1974	Ponderosa pine	4,000 - 5,000
	Douglas-fir	5,000 - 6,000
1975	Ponderosa pine	4,000
1978	Ponderosa pine	3,000 - 5,400
	Douglas-fir	4,000 - 6,000
1980	Douglas-fir	4,500 - 5,500
1982	Douglas-fir	4,500 - 6,000
	Ponderosa pine	4,000 - 5,500

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Note the gap in cone collection between 1965 and 1971. Cone crops, if any, were light and the Forest did not believe there was a need to collect additional seed to supplement the seed inventory during this period. The seed inventory was considered adequate for the artificial regeneration need.

OBSERVATIONS

On the Payette National Forest, ponderosa pine-Douglas-fir appears to have the following cone crop intervals:

Elevation Range	Collectible Cone Crop Interval
3,000 - 4,000	2 to 3 years
4,000 - 5,000	3 to 4 years
5,000 - 6,500	Coincides with an above average crop at the lower elevations

For ponderosa pine at 5,500 to 6,000 feet and Douglas-fir at 6,000 to 6,500 feet, it appears the cone crop must coincide with a heavy to extremely heavy cone crop at the lower elevations before we get a collectible crop at the higher elevation range of these species.

The last heavy crop in ponderosa pine was 1971. Prior to that a heavy crop occurred in 1958, a 13-year interval.

The average ponderosa pine cone crop interval documented currently is 4 to 5 years (Barrett 1979).

TRENDS

With the elevation range of ponderosa pine and Douglas-fir, the trend appears to be: At the lower elevation of a species range, cone crops are 3 to 4 times more frequent than at the higher elevation range.

This trend is supported by the reforestation personnel who have tenure on Districts of the Payette National Forest and have observed cone crops throughout the years. Tenure varies from 10 to 25 years depending on the respective District. Due to the lack of high-elevation seed in the Payette's seed inventory, emphasis has been placed on trying to collect high-elevation seed if cones are available. This trend is not documented by research to my knowledge, but many forests are reporting difficulty in obtaining high-elevation seed for different species due to infrequent cone crops. Research (USDA Forest Service 1965) has documented in Central Idaho that mature and overmature ponderosa pine growing at 5,500 feet produce lower quality seed than similar trees at 4,000 feet.

MANAGEMENT IMPLICATIONS

Cone crops are not uniform in Central Idaho, with variations occurring primarily due to elevation range, tree age and vigor, and soil type.

Schmidt and Shearer (1971) found that 24 out of 25 ponderosa pine seed that reach maturity are eaten by small forest animals. This information was determined over a 6-year period with various cone crops. This, combined with insects feeding on cones and seeds, only leaves seed available for natural regeneration during average or better cone crop years.

The silvicultural and management implications of the above observations and trends are:

1. We have less opportunities for regeneration, both natural and artificial, at the higher elevation of a species range due to longer cone crop intervals.

2. If a cone crop occurs at the higher elevation of a species range, we must not miss the opportunity to collect cones or coordinate site preparation with the crop to achieve natural regeneration.

SUMMARY

Observation and trends in Central Idaho indicate ponderosa pine and Douglas-fir cone crops at the higher elevation range of these species are infrequent. This adds considerable pressure to the timber manager to collect cones at these elevations when a collectible crop does occur, plus accomplish site preparation for natural regeneration with a cone crop.

Managers in areas other than Central Idaho need to ask themselves if they are getting ponderosa and Douglas-fir cone crops at higher elevation ranges. If not, they may want to place more management emphasis on cone collection during a cone crop or site preparation for natural regeneration. Douglas-fir and ponderosa pine may not be the only species with cone crop frequency problems in the higher elevation ranges.

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SEED-DISPERSAL CHARACTERISTICS OF CONIFERS IN THE INLAND MOUNTAIN WEST

Ward W. McCaughey, Wyman C. Schmidt, and Raymond C. Shearer

ABSTRACT: This paper summarizes seed-dispersal characteristics and factors affecting dispersal of the major conifers found throughout the Inland Mountain West. Seed dispersal of these conifers is influenced by a number of physical, climatic, and biotic factors such as seed and wing size, height of cone-bearing trees, distance from seed source, physiographic position, and wind patterns. Birds and mammals also aid in the dispersal of larger seeds, particularly those that are wingless.

INTRODUCTION

Seed-dispersal information can tell us where seed will be dispersed, how much seed can be expected, and when it can be expected. This knowledge, and an understanding of seed germination and seedling survival, provides much of the basic information needed to make valid decisions about regenerating an area. For example, the seed-dispersal characteristics of a species may indicate that adequate seed can be expected throughout an area, and that natural regeneration has a high probability of success.

Conversely, dispersal characteristics may indicate that much of the area is far too distant from a seed source and will have to be artificially regenerated.

Because natural regeneration is often very desirable and practical for many species, seed-dispersal characteristics should be considered in planning regeneration cuttings. This consideration can influence the choice of cutting system such as seed tree, shelterwood, or clearcuttings, the layout and timing of cutting, and site preparations.

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This paper aims at consolidating published and unpublished seed-dispersal information for 23 major conifer species found throughout the Inland Mountain West--that geographic area between the east slopes of the Rockies and east slopes of the Cascades and Sierras in the United States and Canada. Because seed and wing size, height of cone-bearing trees, distance from seed source, physiographic position, and wind patterns also influence seed dispersal, they are also included in this discussion.

SEED DISPERSAL CHARACTERISTICS

Throughout forests of the Inland Mountain West the typical shape of the seed-dispersal pattern for wind-dispersed seeds is a negative exponential curve. Quantity of dispersed seed decreases rapidly as distance from the windward seed source increases and then remains at a low level. The shape of the dispersal curve is much the same at the leeward side of openings, but total distance of dispersal and amount of seed at a given distance from seed source is less than that from the windward edge. Thus, there is a U-shaped distribution of seed dispersal across openings. Some exceptions to this dispersal pattern occur for wingless seeds of juniper (*Juniperus* spp.) and pinyon (*Pinus* spp.), which are dispersed by other modes such as birds, mammals, and gravity.

To provide a basis for comparing dispersal characteristics of nine species, we developed dispersal curves that best fit the variety of available data (fig. 1). Using number of seeds dispersed at the windward timber edge as a species base value, we related the number of seeds dispersed to different distances from the source as a percent of the amount at the timber edge. For species comparison purposes, we used the term "dispersal efficiency," defined as the ratio of number of seeds at the source to the quantity dispersed at a given distance from the source.

A natural logarithm model was used to develop curves for each of the nine species; therefore, curve shapes were similar. However, there were substantial differences in the percent of

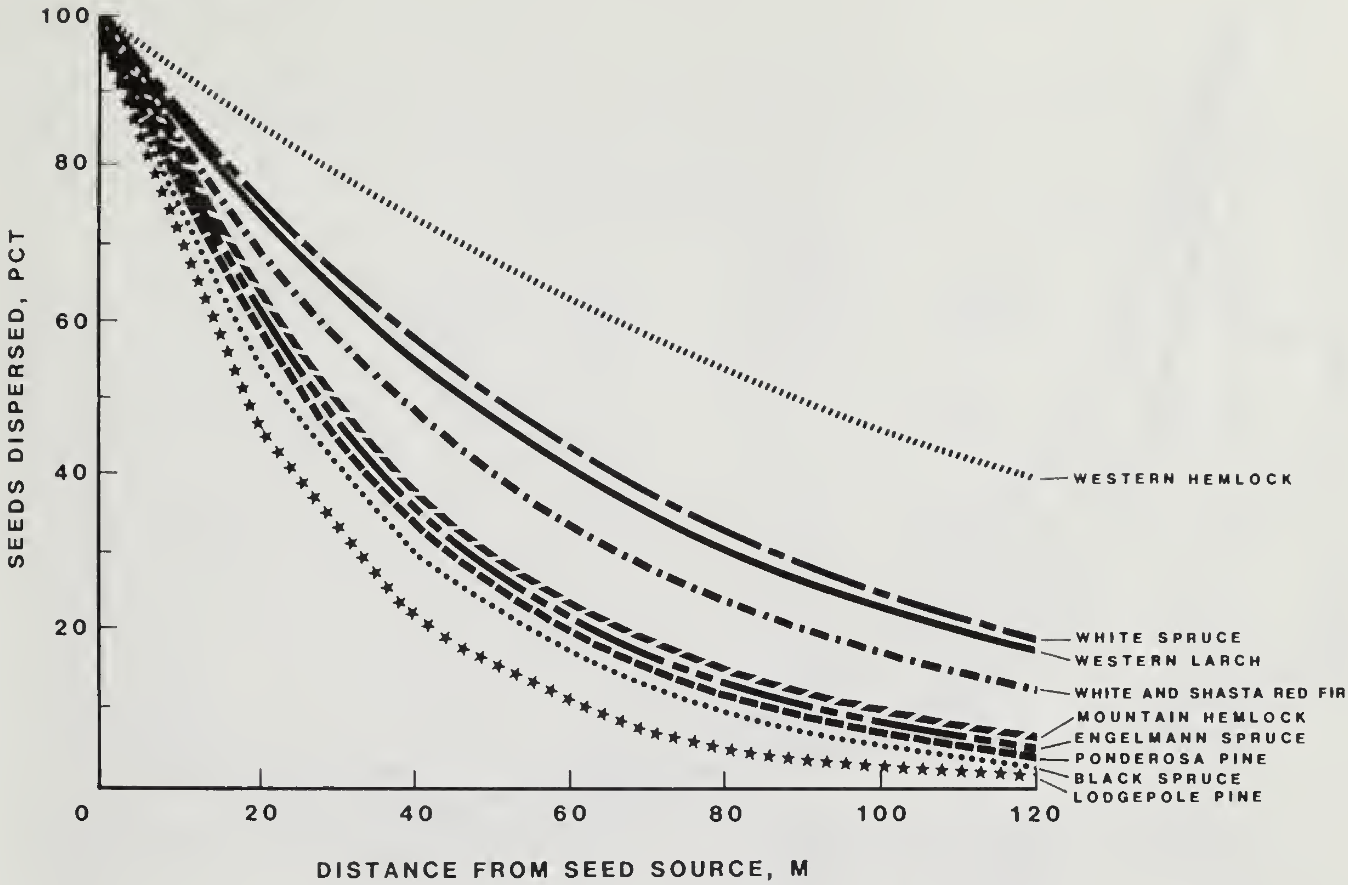

Figure 1.--A comparison of the seed dispersal characteristics of nine conifers of the Inland Mountain West. This relates the number of seeds found at the seed source to the numbers found at increasing distances from the source. Percent values are used to arrive at a common base for the different species.

seeds dispersed to increasing distances. For example, western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) disperses seeds very efficiently but lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) does rather poorly. At 50 m (164 ft), hemlock dispersal was 70 percent while lodgepole pine was only 20 percent of that at the seed source.

It is also apparent that species of the same genus do not necessarily exhibit similar seed dispersal efficiencies. For example, white spruce (*Picea glauca* [Moench] Voss), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and black spruce (*Picea mariana* [Mill.] B.S.P.) range from good to poor in seed dispersal efficiency. The percentage of white spruce seeds reaching 50 m (164 ft) is more than double that of black spruce. Explanations for differences in dispersal efficiencies of these and other species are speculative because definitive data are in short supply.

Mathematical models have been developed for some of the western conifers to illustrate seed dispersal. These models usually fit the data well but offer little explanation of why each species behaves as it does.

Some species, such as Engelmann spruce, have several mathematical models of seed dispersal developed from data collected in different areas within their geographic range (fig. 2). Here, in spite of different independent variables, the dispersal curve shapes are similar. Absolute quantities of dispersed seeds are similar when you consider that one model (Roe 1967) was developed from a bumper crop while the other two models represent several years of seed crop data.

Seed-dispersal patterns of winged-seeded species are influenced by seed and wing length, height and physiographic location of seed source trees, quantity of seed-bearing

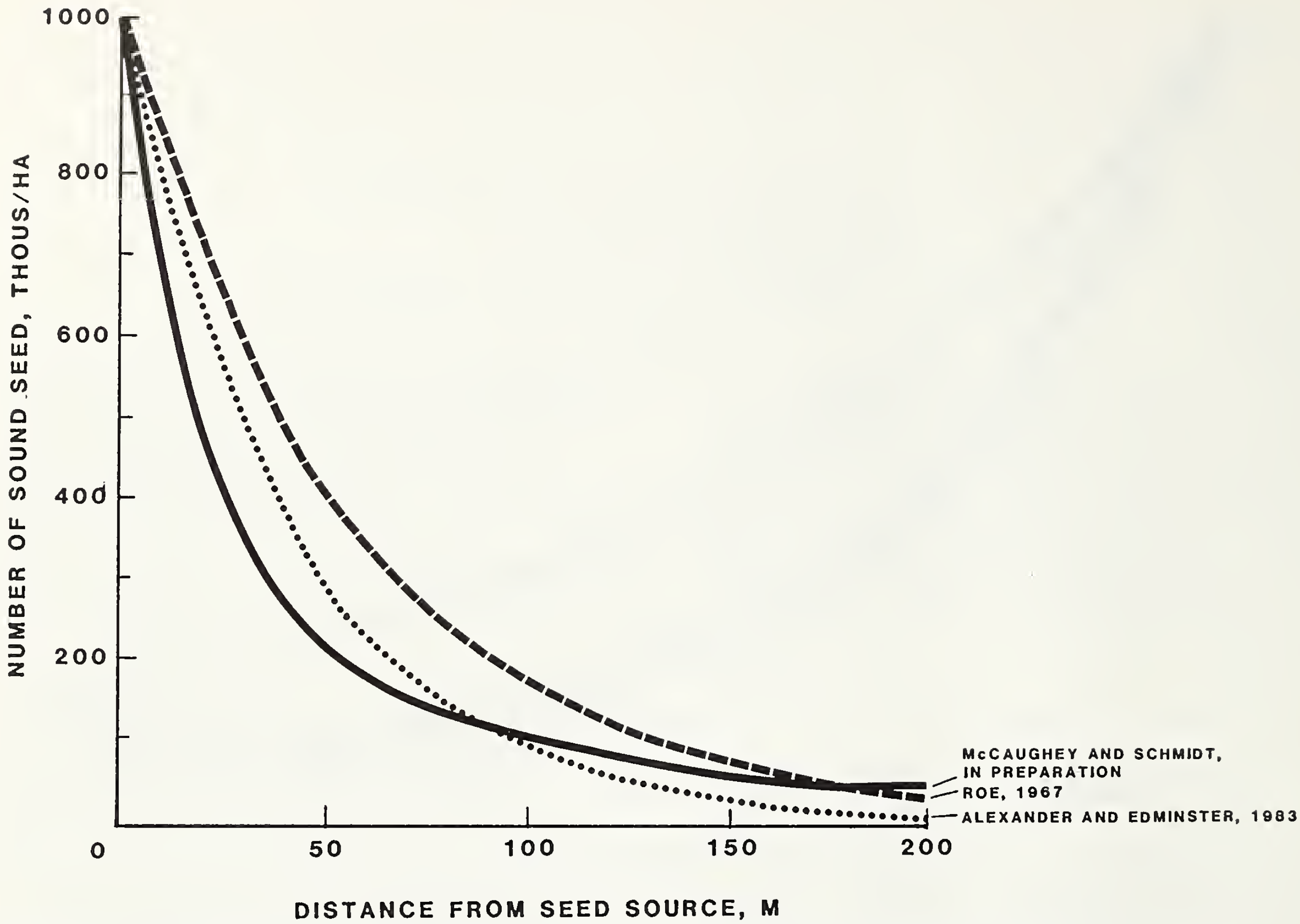

Figure 2.--A comparison of seed dispersal curves from three studies of Engelmann spruce. All three models were calibrated to 1 million seeds per hectare at seed source.

trees, yearly variation of seed production, and time of dispersal. Sharpe and Fields (1982) developed a mathematical model simulating dispersal of winged seeds. Wind speed at the seed source, height of source, and humidity greatly influenced dispersal. Although there are no data to support our claim, small seeds with large wings probably disperse farther than larger seeds with small wings. Seeds likely disperse farther from tall than from short trees and high winds disseminate seeds greater distances than light winds (Isaac 1930). Prevailing winds usually determine the direction of seed dispersal. Rising thermal winds can also disperse seeds uphill in mountainous terrain at mid to lower elevations (Alexander and others 1984; Shearer 1980).

The amount of seed produced is related to the number and character of seed-producing trees. In the Intermountain region the quantity of seed produced was proportional to the square meters of basal area per hectare of Engelmann spruce trees 25.4 cm (10 in) and larger in diameter (Roe 1967; McCaughey and Schmidt in preparation). Each species differs in the frequency of heavy, moderate, and light seed crops. The period between heavy seed crops for various species ranges from about 3 to 10 years. Sound seed production increases linearly with total seedfall, although there is considerable variability between years and locations (Alexander and others 1982).

The following sections present brief descriptions of seed dispersal for each of 23 conifers found within the Inland Mountain West. Table 1 presents descriptions of seed characteristics and cone phenology.

Table 1.--Seed characteristics and tree phenology of some conifers of the Inland Mountain West

Species	Seed characteristics[1]			Phenology[2]	
	Seed length	Wing length	Average number of seeds per kilogram	Cone ripening dates	Primary seed dispersal dates
	mm	mm	Thousands		
Abies					
Grand fir	9.5	19.0	40.6	Aug.	Aug.-Sept.
Subalpine fir	-	-	76.7	Aug.	Sept.-Oct.
White fir	12.7	-	24.5	Sept.-Oct.	Sept.-Oct.
Juniperus					
Rocky Mountain juniper	[3]6.4	none	59.7	Sept.-Dec.	Oct.[4]
Western juniper	-	none	27.1	Sept.	Extended[4]
Larix					
Subalpine larch	-	-	313.1	Aug.-Sept.	Sept.
Tamarack	3.2	6.4	701.1	Aug.-Sept.	Sept.-Spring
Western larch	6.4	12.7	302.0	Aug.	Sept.-Oct.
Picea					
Black spruce	3.2	6.4-9.5	890.1	Sept.	Oct.[5]
Blue spruce	-	-	233.4	Fall	Fall-Winter
Engelmann spruce	3.2	12.7	297.6	Aug.-Sept.	Sept.-Oct.
White spruce	3.2	6.4-9.5	498.2	Aug.	Sept.
Pinus					
Jack pine	2.1	8.5	288.8	Sept.	Sept.[6]
Limber pine	-	-	10.8	Aug.-Sept.	Sept.-Oct.
Lodgepole pine	4.2	12.7	207.2	Aug.-Sept.	Sept.-Oct.[6]
Pinyon	-	-	4.2	Aug.-Sept.	Sept.-Oct.
Ponderosa pine	6.4	25.4	26.5	Aug.-Sept.	Aug.-Sept.
Western white pine	8.5	25.4	59.5	Aug.	Aug.-Sept.
Whitebark pine	-	-	5.7	Aug.-Sept.	Oct.[7]
Pseudotsuga					
Douglas-fir (interior)	-	-	85.5	July-Aug.	Aug.-Sept.
Thuja					
Western redcedar	3.2	3.2	912.7	Aug.-Sept.	Aug.-Sept.
Tsuga					
Mountain hemlock	3.2	12.7	251.5	Aug.-Oct.	Sept.-Oct.
Western hemlock	1.6	-	573.2	Aug.-Oct.	Sept.-Winter

[1]Information from: USDA Forest Service 1974; Harlow and others 1979.

[2]Information from: USDA Forest Service 1965; USDA Forest Service 1974; Schmidt and Lotan 1980.

[3]Cone is 6.4 mm in diameter and has one or two, rarely three or four seeds.

[4]Cones may persist on trees for 2 to 3 years.

[5]Black spruce retains its cones in a semiserotinous state for several years providing a continuous source of seed in stands over 40 years old.

[6]Many serotinous cones remain closed for several months or years.

[7]Seeds are dispersed when the detached cone disintegrates.

Abies

Grand fir.--Wind disperses grand fir (*Abies grandis* [Dougl. ex D. Don] Lindl.) seed in early fall as cones disintegrate and fall from the tree. The seeds are large, and as a result dispersal distances are relatively short. Haig and others (1941) report that fir seed disperses up to 122 m (400 ft) from the source, but 46 to 61 m (150 to 200 ft) was the average dispersal distance. On steep topography of a western Montana site, grand fir seed dispersed upslope nearly 244 m (800 ft) from the nearest source (Shearer 1985).

Grand fir seed dispersal follows the same patterns as the species shown in figure 1. Eight-year results of seed production studies in Idaho showed that grand fir produced the least amount of seed of the species associated with western white pine (USDA Forest Service in press).

Subalpine fir.--Subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) seed is wind-disseminated. Prevailing winds have been found to carry seeds up to 80 m (264 ft) from the windward edge of openings in Colorado (Noble and Ronco 1978). In Montana, Shearer (1980) found that thermal upslope winds dispersed fir seed uphill into clearcuts.

Seed dispersal of subalpine fir follows the typical wind-dispersal pattern (fig. 1). In clearcut openings in Colorado, quantity of seed declined rapidly to about 30 m (100 ft), and then remained at low levels to 80 m (264 ft) from the timber edge (Noble and Ronco 1978). Dispersed seed quantities increase at about 10 m (33 ft) from the leeward edge of the opening, giving a U-shaped distribution profile of dispersal across the openings.

Nobel and Ronco (1978) reported that the velocity of prevailing winds, amount of seed produced, and distance from the source influenced subalpine fir seed dispersal into openings in Colorado. In the mountains of Montana, peak dispersals were usually associated with upslope winds, temperatures greater than average, and humidity levels lower than average (Shearer 1980).

White fir.--White fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.) seed is wind-disseminated as cones disintegrate on the tree in September and October (USDA Forest Service in press). Some seed disperses at least 114 m (375 ft) from the source into openings (Franklin and Smith 1974b). Because fir seed wings are short and broad in relation to seed size, dispersal distances are thought to be small (Gordon 1970; Siggins 1933).

In Oregon, the quantity of white fir seed decreased rapidly from the windward source out to 38 m (125 ft) and then leveled off. Dispersed seed quantities averaged about 25 and 10 percent at 38 m (125 ft) and 114 m (375 ft), respectively, of amounts at the windward source (Franklin and Smith 1974b).

Some white fir seed is dispersed by animals such as the Douglas' squirrel (*Tamiasciurus douglasii* spp.), which cuts and caches fir cones before disintegration (Fowells and Schubert 1956).

Distance was the only measured factor that affected white fir seed dispersal. The quantity dispersed was significantly correlated with distance from the stand edge (Franklin and Smith 1974b). Although only 20 to 50 percent of fir seeds are sound, even in good production years, no significant differences in dispersal distances of sound and empty seeds have been detected (USDA Forest Service 1965; Franklin and Smith 1974b).

Juniperus

Rocky Mountain juniper.--The fruits of Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) are small, indehiscent strobili called "berries" that contain one to four, rarely as many as 12, brownish seeds (USDA Forest Service 1974). The berries are heavy and normally fall close to the parent tree accounting for the slow expansion of juniper forests (Burkhardt and Tisdale 1969). Most of the fruit remains on the tree until late spring. However, after fall ripening, birds and animals have ample time to use it as a food supply. Seed quickly passes through the digestive tracts of birds and animals with little effect on germination capability. Randles (1949) reported that turkeys help disseminate juniper seeds in the Southwest as do bighorn sheep, chipmunks, foxes, and some small mammals. Dispersal of juniper seed depends upon the movement patterns of animals that use the berries as a food source (Randles 1949). The Bohemian waxwing (*Bombycilla garrulus* [Linnaeus]) can eat more than 900 seeds a day and spread them over a wide area (Phillips 1910).

Western juniper.--The fruits of western juniper (*Juniperus occidentalis* Hook.) are small "berries" that contain one to four, rarely as many as 12, brownish seeds. Dispersal occurs when the berries fall off the trees, but usually birds or other animals eat the fruit and disperse the seeds via their excrement (USDA Forest Service 1974). Seedlings are found along fence rows, where they are closely spaced as in a hedge, indicating

that seeds were bird-dispersed. Groups of juniper seedlings are also found beneath other trees to which birds apparently carried juniper seed (USDA Forest Service 1965). Specific information is limited on the types of animals that disperse western juniper seed and how far these animals carry the seed.

Larix

Subalpine larch.--Little is known about seed-dispersal distances of subalpine larch (*Larix lyallii* Parl.). The relatively lightweight, winged seeds fall from the cones in September and are wind-disseminated (USDA Forest Service 1974). Good seed crops occur about once every 10 years. Therefore, seedling establishment is sporadic and limited (USDA Forest Service in press).

Tamarack.--Little information is available on the seed-dispersal characteristics of tamarack (*Larix laricina* [Du Roi] K. Koch). Duncan (1954) reports large numbers of tamarack seedlings located within 1 tree height, a moderate number within 2 tree heights from the seed source, but only scattered seedlings at greater distances. This short dispersal distance is probably explained by the fact that mature seed-producing trees average only 15 to 25 m (50 to 80 ft) tall. Because tamarack seed is winged and wind-dispersed, we assume it follows the same distributional pattern as other wind-dispersed species (fig. 1). Characteristically, tamarack grows in low flat areas, making topographic influences, so common with other western conifers, of lesser consequence. Tamarack seeds are also dispersed by red squirrels (*Tamiasciurus hudsonicus* [Erxleben]), which cut cone-bearing branchlets and cache the cones (Duncan 1954).

Western larch.--Western larch (*Larix occidentalis* Nutt.) seed is small, enabling it to wind-disperse long distances from the source (USDA Forest Service 1965). Numerous studies in Montana have indicated that larch seed disperses at least 250 m (800 ft)(Boe 1953; Shearer 1959; Schmidt and others 1976; Shearer 1985).

The amount of sound larch seed dispersing from the source into clearcuts decreases rapidly out to 122 m (400 ft), and then remains at a low level. Seed crops vary substantially by year, which affects the dispersal pattern. In poor seed years, dispersal beyond 80 m (264 ft) from the timber edge is usually not detected with normal sampling procedures.

Thermal upslope winds in mountain terrain have a direct effect on larch seed dispersal in cuttings on mid to lower elevation slopes in early fall. Cones on upper elevation slopes mature 2 to 4 weeks later than at mid to lower elevations (Fiedler 1976). Therefore, seed is not released during the early fall when thermal upslope winds are prevalent. As a result a high proportion of larch seed on upper slopes is dispersed by storm fronts in mid to late fall (Shearer 1985).

Picea

Black spruce.--The maximum dispersal distance of black spruce (*Picea mariana* [Mill.] B.S.P.) seed is about 100 m (328 ft) from the source (LeBarron 1939; Payandeh and Haavisto 1982). LeBarron (1948) reported that although seed disperses more than 91 m (300 ft) from a source, the number of dispersed seed at 30 m (100 ft) is only 6 percent of the amount of seed falling in the uncut timber.

Dispersal is also affected by windspeed and direction, time of release, and physiographic location, but distance is the only factor that has been quantified. Payandeh and Haavisto (1982) showed that the two variables, stripcut width and distance from the windward stand edge, were highly correlated with the quantity of spruce seed dispersed across a clearcut.

Blue spruce.--We found no specific studies that described seed dispersal of blue spruce (*Picea pungens* Engelm.). Shepperd (1985) speculated that because blue spruce seed is slightly larger than Engelmann spruce, dispersal distances are less. The effective seeding distance, of blue spruce, to obtain adequate natural regeneration, probably is about three to four times the height of the seed-bearing trees.

Engelmann spruce.--Wind, the main disseminator of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) seeds, carries seeds to distances of 244 m (800 ft) from the uncut timber bordering the windward edges of clearcuts (USDA Forest Service in press). In the Intermountain area, wind commonly disseminates spruce seeds to distances of 201 m (660 ft) from the source (Squillace 1954; Roe 1967; McCaughey and Schmidt in preparation). These distances were similar to distances reported for clearcuts in Colorado (Alexander and Edminster 1983). Seeds have also been observed skidding great distances over a glazed snow surface.

General patterns of spruce seed dispersal across clearcuts are shown in figure 2. After an initial rapid decline, the quantity dispersed levels off or gradually declines beyond 100 m (348 ft) from the seed source (Noble and Ronco 1978; Roe 1967). The quantity of dispersed seed increases again at about 10 m (33 ft) from the leeward edge, producing a U-shaped dispersal pattern across openings (Noble and Ronco 1978). Alexander and Edminster (1983) reported that, in Colorado, nearly 40 percent of the spruce seedfall under the uncut windward stand dispersed about 30 m (100 ft), and 10 percent dispersed 91 m (300 ft) from the source. Similar results were found in the Intermountain region where dispersed seed quantities started leveling off at about 120 m (394 ft) from the source (McCaughey and Schmidt in preparation).

Distance from seed source had the greatest impact on the dispersal patterns of Engelmann spruce (fig. 2)(Roe 1967; Noble and Ronco 1978; Alexander and Edminster 1983; McCaughey and Schmidt in preparation). Also, studies in the Intermountain area show that quantity of seeds dispersing into clearcuts is strongly correlated with basal area of mature spruce in the adjacent uncut timber. As stand basal area of mature spruce 25 cm (10 in) and larger increased, quantity of dispersed seed increased (Roe 1967; McCaughey and Schmidt in preparation). Colorado studies also show a strong positive correlation of seedfall under the uncut stand with quantity dispersed into clearcuts (Alexander and Edminster 1983; Noble and Ronco 1978).

White spruce.--White spruce (*Picea glauca* [Moench] Voss) has very small seeds, which wind disperse in the air and over snow. Early studies indicated 101 m (330 ft) was the greatest distance seeds disseminated via air, but with sufficient wind much greater distances would be expected (Rowe 1955). Late-falling seeds were blown considerable distances over crusted snow (Rowe 1955). Nearly 88 percent of seeds fall in September, the first month of dispersal, with the remaining seeds dispersing during the winter and spring (Crossley 1955). About 20 percent of the total seeds dispersing during the winter were trapped beyond 100 m (328 ft), and 9 percent beyond 200 m (656 ft) from the source. The presence of seedlings indicated that spruce seed dispersed at least 300 m (984 ft) from the stand edge in strip and clearcuttings (Dobbs 1976).

Quantity of dispersed spruce seed decreases rapidly from timber edge to about 140 m (460 ft) into clearcuts, and then levels off for a considerable distance from the source. This pattern suggests that significant quantities of seed are released in high winds (Dobbs 1976).

Pinus

Jack pine.--Jack pine (*Pinus banksiana* Lamb.) has two seed dispersal modes because its cones are serotinous and nonserotinous. Although seeds are winged and small, about 2.1 mm (0.33 in) long, they have a relatively short dispersal distance. We found no studies that described seed dispersal from nonserotinous cones. However, indirect evidence of dispersal through seedling establishment suggests the effective dispersal range is about 34 to 40 m (110 to 130 ft)--2 tree heights--but, the number of established seedlings more than 1 tree height from the seed source is low (USDA Forest Service 1939). Seed dispersal distances from serotinous cones are very short because cones must be near the ground surface before ambient air temperatures are high enough to melt the resin bond. Cameron (1953) reported that the bonding resin on serotinous cones melts at about 50 °C (122 °F).

Limber pine.--Limber pine (*Pinus flexilis* James) seeds are very large and have rudimentary wings or are wingless (Harlow and others 1979). Because of their large size, they are seldom dispersed by wind. The primary disperser in northern Utah, Wyoming, and Arizona (and presumably throughout the range of limber pine) is the Clark's nutcracker (*Nucifraga columbiana* [Wilson])(Tomback and Kramer 1980; Benkman and others 1984). Nutcrackers carry seeds to caches under forest litter. Some of these cache sites are favorable to germination (Tomback 1981). Red squirrels cache cones under deep litter piles where seeds are unlikely to germinate (Benkman and others 1984). Presumably, birds can disperse these seeds great distances, but animal, wind, and gravity dispersal likely provide limited distribution.

Lodgepole pine.--Lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) has the smallest seeds of any pine except jack pine. Yet, dispersal distances are far less than such associates as western larch and Engelmann spruce. Seeds from nonserotinous cones, sufficient to restock cutover areas, seldom disperse over 61 m (200 ft) from the source (Boe 1956; Perry and Lotan 1977a). However, in western Montana, winds dispersed seeds uphill nearly 244 m (800 ft) from the downhill side of clearcuts (Shearer 1985). Seeds have been observed skidding great distances over a glazed snow surface.

Dispersal distances for seeds from serotinous cones depend upon the distance cones are scattered during logging. Serotinous cones need temperatures near 60 °C (140 °F) to break resin bonds. Fire will easily melt the resin bond, but cones must be within 30 cm (12 in)

of the ground before ambient air temperatures are high enough to open the cones (Perry and Lotan 1977b; Lotan and Perry 1983). Eighty-three percent of serotinous cones on south slopes and 40 percent on north slopes open when they are less than 30 cm (12 in) above the ground (Lotan 1964).

Quantity of lodgepole seed decreases rapidly as distance from the source increases--at 20 m (66 ft) into clearcuts seedfall varies from about 10 to 30 percent of that at timber edge (Boe 1956; Dahms and Barrett 1975; Lotan and Perry 1983). At 20 m (66 m) from the windward side (fig. 1) the seedfall is about 45 percent of that at stand edge. A U-shaped distribution occurs between stand edges across clearcuts (Lotan and Perry 1983).

Wind disperses lodgepole seeds from nonserotinous cones, but seed from serotinous cones is usually dispersed by scattering conebearing slash throughout logging areas. Seed dispersal distances are likely to be greater on south than on north slopes because of higher velocities of thermal upslope winds on warmer south-facing slopes (Fiedler 1974).

Pinyon.--Seed dispersal characteristics are similar for pinyon (*Pinus edulis* Engelm.) and singleleaf pinyon (*Pinus monophylla* Torr. and Frem.), therefore, they are presented together.

The large seeds of pinyon are dispersed by gravity or animals since the seed wing is easily detached, and of no practical use in dispersal (Phillips 1909). Clark's nutcrackers cache seeds long distances from the source, 1 to 3 cm (.4 to 1.2 in) below the soil surface in open areas (Vander Wall and Balda 1977; Lanner and Vander Wall 1980). Some cached seeds, not utilized by nutcrackers during the winter months, germinate and thus expand pinyon distribution. Everett (1985) speculates that rodents disperse seed locally under, or short distances from, existing pinyon stands. Preliminary results indicate that nearly 87 percent of seedlings are located under or near fully stocked stands. Rasmussen (1941) reported that woodrats (*Neotoma* spp.), mice (*Peromyscus* spp.), and chipmunks (*Eutamias minimus* spp.) cached pinyon seeds, but whether caches were on sites favorable for germination was unknown.

Ponderosa pine.--Seed dispersal information presented here is for ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), since little information is available for Arizona pine (*Pinus ponderosa* var. *arizonica* [Engelm.] Shaw) and Rocky Mountain ponderosa pine (*Pinus ponderosa* var. *scopulorum* Engelm.).

Ponderosa pine seeds are fairly large, and as a result do not disseminate great distances (Barrett 1966). Theoretical calculations of seed flight indicated that a 30-m (100-ft) tree exposed to 32-km/h (20-mi/h) winds would disperse seeds up to about 180 m (594 ft) (Siggins 1933). Data indicate that most seeds fall within 20 to 40 m (60 to 132 ft) from seed-producing trees (Curtis and Foiles 1961; Barrett 1966). However, a minor amount of seed will disperse up to 160 m (528 ft) in central Oregon and 244 m (800 ft) in western Montana (Barrett 1966; Shearer 1985). In Idaho, 82 percent of the seed dispersed within 152 m (500 ft) of the timber edge was confined to 30 m (100 ft) of the edge. Some of the seed falls to the ground in cones (USDA Forest Service 1940). Seed is released when high ground temperatures dry out the cones causing scales to open (Curtis and Foiles 1961).

Western white pine.--Western white pine (*Pinus monticola* Dougl. ex D. Don) seed is mainly wind dispersed, although squirrels, mice, and birds disseminate some seed. Clumps of seedlings have been found where seeds cached by mice have germinated (USDA Forest Service 1965). Seeds are large and do not disperse great distances. Haig and others (1941) reported that seed sufficient for adequate reproduction seldom reaches more than 122 m (400 ft) from the source. Isaac (1930) demonstrated that when white pine seed was dropped from a height of 61 m (200 ft), in a 21 km/h (13 mi/h) wind, it dispersed 792 m (2,600 ft) from the point of release. Shearer (1985) reported that white pine seeds dispersed at least 244 m (800 ft) uphill from the source at the bottom edge of steep mountain clearcuts in Montana.

Whitebark pine.--Little information is available on the seed-dispersal characteristics of whitebark pine (*Pinus albicaulis* Engelm.). Its large seeds are wingless and disseminate after the cones detach from the tree and disintegrate (USDA Forest Service 1974). The primary disseminators are animals, especially the Clark's nutcracker. A single nutcracker eats up to 32,000 seeds per year. These birds store whitebark seeds in small caches on the ground, some on microsites favorable for germination. This dispersal by nutcrackers helps maintain the "pioneering" status of whitebark pine (Tomback 1981).

Squirrels also collect and cache whitebark pine cones and seeds, often carrying them great distances from the source. Bears also feed on the seeds, especially grizzly bears (*Ursus arctos* [Linnaeus]), which depend heavily on these seeds as an important source of energy, particularly in the Yellowstone

ecosystem. Some seeds pass through the bear's digestive system intact; therefore, bears may serve as a minor mode of dispersal.

Pseudotsuga

Rocky Mountain Douglas-fir.--Rocky Mountain (interior) Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco) has moderate-size seeds and seed wings and is wind-disseminated. Boe (1953) reports that large quantities of seeds dispersed up to 80 m (264 ft) from the source in clearcuts on the Coram Experimental Forest in northwestern Montana. Seed also disperses into clearcuts on steep topography up to 244 m (800 ft) uphill from the source (Shearer 1985). Reproduction indicates a seed-dispersal radius of about 91 to 183 m (300 to 600 ft) around open-grown trees on level land (Frothingham 1909).

Douglas-fir has a seed-dispersal pattern similar to other species (fig. 1). Quantity of dispersed seed decreases rapidly out to 80 m (264 ft) and remains at low levels from 80 to 241 m (264 to 792 ft) from the source (Boe 1953). Shearer (1985) reported that early-ripening seeds were dispersed by upslope thermal winds and late-ripening seeds by winds of unstable air masses from storm fronts.

Thuja

Western redcedar.--Western redcedar (*Thuja plicata* Donn ex D. Don) seed is wind-disseminated, but because of a small wing surface, its rate of fall is fast and flight distance is short (Siggins 1933). Isaac (1930) reports that seed did not disperse more than 122 m (400 ft) when released at 46 m (150 ft) above the ground. However, in British Columbia, an examination of regeneration indicated that seed dispersed at least 201 m (660 ft) from the source (Clark 1970).

The pattern of redcedar seed dispersal is apparently similar to patterns shown for other conifer species (fig. 1). Nearly 80 percent of filled seeds in clearcuts are found within 15 to 30 m (50 to 100 ft) from the source. (Gashwiler 1969). Seeds, dispersed between 61 to 76 m (200 to 250 ft) from the source, accounted for 17 percent of the total seed count in clearcuts with only 4 percent dispersing 107 to 122 m (350 to 400 ft).

Tsuga

Mountain hemlock.--Seeds of mountain hemlock (*Tsuga mertensiana* [Bong.] Carr.) are small, and have a large wing, making them well-suited for wind dispersal. Mountain hemlock is a prolific seed producer and bears seed nearly every year (USDA Forest Service 1965). Its seed disperses at least 114 m (375 ft) into clearcuts from the source (Franklin and Smith 1974a).

The dispersal pattern of mountain hemlock is very similar to Engelmann spruce (fig. 1). Quantity of hemlock seed decreases rapidly from the source out to about 38 m (125 ft), and then levels off at a low level or decreases slowly from 38 to 114 m (125 to 375 ft) (Franklin and Smith 1974a). The amount of seed dispersed at 120 m (394 ft) from the source is less than 10 percent of that at the source (fig. 1).

Mature seed-producing trees are relatively short, usually 15 to 23 m (50 to 75 ft). Were it not for this, seed-dispersal distances would likely be much greater. The number of seed-bearing trees in adjacent stands also influences the amounts of seed dispersed into clearcuts (Franklin and Smith 1974a).

Western hemlock.--Western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) seeds are light and are dispersed great distances by wind. During bumper crop years, enough seed falls within 100 m (330 ft) from the source to provide optimum seedling establishment (Clark 1970). To produce sufficient seed for adequate stocking 201 m (660 ft) from the source, at least two bumper seed crops are usually required.

Considerable amounts of hemlock seed have been observed dispersing up to 610 m (2,000 ft) from the source. In a controlled test, hemlock seeds released at a height of 61 m (200 ft) in a 20.1 km/h (12.5 mi/h) wind dispersed as far as 1 158 m (3,800 ft)(Isaac 1930). In our comparisons of dispersal curves (fig. 1), western hemlock stood out as the most efficient of the western conifers. For example, the number of seeds dispersed to 120 m (394 ft) was nearly half of the number dispersed to the stand edge. This was about double that of any other associated species.

Hemlock seed disseminates from cones throughout fall and early winter months. During the winter, winds sometimes disperse seeds across crusted snow, depositing large amounts in small depressions (Harris 1969).

DISCUSSION

Managers depending on natural regeneration in their silvicultural practices should consider seed dispersal characteristics in their plans. This paper synthesizes information available for our western conifers. Of this information, the following factors stand out as being very important in describing seed dispersal:

1. Wind is the primary dispersing mechanism for seeds of western conifers.

2. The shapes of seed dispersal curves are very similar for most western conifers, but species vary substantially in dispersal distances.

3. Of the tree, stand, and site characteristics that largely determine the dispersal patterns of western conifers, several stand out:
   - seed aerodynamics
   - tree height
   - time of dispersal
   - character of the seed-producing stand (size and number of each species)
   - annual variability of seed production
   - physiographic position of seed source as related to wind character.

4. Thermal winds are very important for early season dispersal of seeds; prevailing winds and storm fronts are very important for late season dispersal.

5. Most seeds are dispersed through the air in the fall, but seeds released in late fall and early winter may also be blown over crusted snow.

6. Birds and mammals are the primary dispersal agents for wingless seeds and can carry them for substantial distances.

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CONE PRODUCTION ON DOUGLAS-FIR AND WESTERN LARCH IN MONTANA

Raymond C. Shearer

ABSTRACT: This study determined the number of cones that matured on Douglas-fir and western larch growing on twenty 0.1-ha (0.25-acre) plots from 1980 through 1983 at each of four locations near Missoula, MT. A good cone crop in 1980 produced 80 percent of all cones counted during the 4-year study. In 1980, cones were produced on 45 percent of the Douglas-fir and 38 percent of the larch in the 10- to 15-cm (4- to 6-inch) diameter class while 85 percent were produced by both species in the 30- to 36-cm (12- to 14-inch) diameter class. The average number of cones per tree in 1980 increased 10 times for Douglas-fir and 27 times for larch as the diameter classes increased from 10 to 15 cm (4 to 6 inches) to 30 to 36 cm (12 to 14 inches). In years of fair or poor cone production the average number of cones per tree was about seven times greater for Douglas-fir and 15 times greater for western larch in the 30- to 36-cm (12- to 14-inch) diameter class than in the 10- to 15-cm (4- to 6-inch) diameter class. More than half of the Douglas-fir and larch in the 10- to 15-cm (4- to 6-inch) diameter class failed to produce any cones during the study; only 7 percent of the trees in the 30- to 36-cm (12- to 14-inch) diameter class failed to produce cones.

INTRODUCTION

Cone production in natural forest stands has been studied at several locations in the Inland Mountain West (Fowells and Schubert 1956; Franklin and others 1974; Alexander and Noble 1976). Cone production of conifers native to Montana was studied by Boe (1954). He classified Rocky Mountain Douglas-fir (Pseudotsuga menziesii var. glauca [Beissn.] Franco) west of the Continental Divide as a prolific seeder and western larch (Larix occidentalis Nutt.) as a good seeder.

Cone production either on individual trees or within natural stands usually varies greatly by year. Because Douglas-fir and larch cones develop throughout the crowns, trees of greater diameter and crown volume usually produce more cones (Fowells 1965). The purpose of this study was to determine for Douglas-fir and larch at four study sites in western Montana from 1980 through 1983: (1) the influence of insect larvae, particularly western spruce budworm (Choristoneura occidentalis Freeman), on cone and seed losses (Hedlin and others 1980) and (2) the number of cones produced each year. Shearer (1984) published information on the cone and seed reduction caused by insect feeding. This paper reports the number of cones that were produced on the Douglas-fir and larch growing within each of 80 plots.

STUDY SITES

In 1980, four study sites were selected near Missoula in western Montana. Two were in the warm and dry Douglas-fir forest series and two in the cooler and moister subalpine fir (Abies lasiocarpa [Hook.] Nutt.) forest series (Pfister and others 1977):

Forest series	Distance and direction of sites from Missoula, MT
Douglas-fir	Ashby Creek (Ashby) 29 km (18 miles) east
	Blue Mountain Road (Blue) 8 km (5 miles) southwest
Subalpine fir	West Fork Lolo Creek (Lolo) 35 km (22 miles) southwest
	Spring Creek (Spring) 60 km (36 miles) northeast

The study sites are identified hereafter by the names in parentheses.

Ashby is a second-growth stand averaging 50 years old, composed of 35 percent Douglas-fir, 24 percent western larch, 20 percent Rocky Mountain ponderosa pine (Pinus ponderosa var. scopulorum Engelm.), and 21 percent lodgepole pine (P. contorta var. latifolia Engelm.). Blue, a partially cut stand averaging 80 years old, is composed of 67 percent Douglas-fir, 29 percent western larch, and 4 percent ponderosa pine. Lolo, a partially cut stand averaging 70 years of age, is composed of 15 percent Douglas-fir, 35 percent western larch, 48 percent lodgepole pine, and 2 percent ponderosa pine, Engelmann spruce (Picea engelmannii Parry ex Engelm.), and subalpine fir. Spring is a more open partially cut stand with trees ranging from 60 to 175 years of age. Composition of the

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cone-bearing trees is 30 percent Douglas-fir, 42 percent western larch, 13 percent subalpine fir, 8 percent lodgepole pine, 6 percent Engelmann spruce, and 1 percent ponderosa pine.

At each of these four study sites, twenty 0.1-ha (0.25-acre) circular plots were randomly established. All trees 8 cm (3 inches) d.b.h. and larger were numbered. Trees were grouped into 5-cm (2-inch) diameter classes for this paper: 10 cm [10.2-15.0] (4-inch) [4.0-5.9], 15 cm [15.2-20.1] (6-inch) [6.0-7.9], for example. Broader groupings were also used; for example, 10-15 cm (10.2-20.1 cm) [4-6 inch (4.0-7.9 inch)] and 20-25 cm (20.2-30.2 cm) [8-10 inch (8.0-11.9 inch)].

The number of trees per acre was greatest at Blue, followed by Lolo, Ashby, and Spring (table 1). Each location had both Douglas-fir and larch in the 10- through 36-cm (4- through 14-inch) diameter classes. Douglas-fir and western larch were most abundant in the 15-cm (6-inch) diameter class at each location. Only occasional larger diameter trees grew within the plots.

Table 1.--Average number of Douglas-fir (PSME), western larch (LAOC), and other trees per acre by diameter class, forest series, and study area in western Montana, 1980. Basis: twenty 0.1-ha (0.25-acre) plots at each location

Diameter class	PSME	LAOC	Other	PSME	LAOC	Other
	Pseudotsuga menziesii Forest Series					
	Ashby Creek			Blue Mountain		
4	7.4	3.8	0.8	7.6	6.4	
6	19.8	13.2	18.6	50.8	20.4	3.0
8	10.6	8.4	14.0	40.6	16.2	1.8
10	6.2	5.0	10.2	23.4	9.2	1.4
12	3.6	2.2	7.4	6.6	4.2	.6
14	.8	1.0	4.0	1.2	.6	.2
16	.4		1.4	.2	.2	.4
18	.2		1.0			
20			.4			.2
Sum	49.0	33.6	57.8	130.4	57.2	7.6
	Abies lasiocarpa Forest Series					
	Lolo Creek			Spring Creek		
4	1.0	1.0	1.4	7.2	3.2	6.6
6	11.4	28.0	35.2	7.6	15.4	7.8
8	5.0	17.6	27.4	3.8	9.8	3.6
10	3.4	6.4	13.8	3.6	1.6	3.6
12	2.6	3.4	4.8	.6	3.2	.6
14	.4	1.0	.2	.6	.4	.2
16	.2	.6				
18	.2			.6		
22		.4				
30		.4				
Sum	24.2	58.8	82.8	24.0	33.6	22.4

The Blue study area had 1.1 to 2.8 times more total basal area than the other three locations; Spring had only 0.4 as much as the other sites (table 2). Blue had from 2.7 to 6.0 times more Douglas-fir basal area and from 0.9 to 1.8 times more larch than the other stands.

Table 2.--Basal area (ft^2/acre) of Douglas-fir (PSME), western larch (LAOC), and other trees by forest series and study area in western Montana, 1980. Basis: twenty 0.1-ha (0.25-acre) plots at each location

Forest series	Plot	PSME	LAOC	Other	Total
Douglas-fir	Ashby	20.1	13.9	34.1	68.1
	Blue	54.7	24.2	4.4	83.2
Subalpine fir	Lolo	11.0	27.8	34.5	73.3
	Spring	9.1	13.1	7.5	29.7

CONE PRODUCTION ESTIMATES

Douglas-fir and western larch cone production was estimated in 1980, 1981, 1982, and 1983 on the 80 plots by counting the fully elongated cones between late July and early September. No attempt was made to judge the amount of cone mortality from bud burst to the time of examination. Cone counts on trees of other coniferous species growing on the plots were not made.

In 1980, counts were made from a truck-mounted hydraulic bucket. In 1981, 1982, and 1983, cones were counted on each tree from points where the full length of the tree could be scanned with binoculars. Trees that produced no or few cones (usually less than 10 cones), were carefully examined to be sure no cones were missed. This meant observing these trees from two or more locations so the entire crown could be scanned. Trees with greater numbers of cones were examined from only one location.

RESULTS

The average total number of mature cones per tree counted from 1980 through 1983 varied by species and by study location (table 3). Douglas-fir averaged greater total 4-year cone production than western larch at Ashby, Lolo, and Spring. These numbers were substantially lower than the potential because of insect-caused mortality in the early development of the conelets (Shearer 1984). Cone production of both species was greatly influenced by year and diameter class.

Table 3.--Average number of Douglas-fir and western larch cones per tree and number of trees sampled per year by study area, western Montana

Year	Study area	Douglas-fir: Average and standard deviation	Douglas-fir: Trees	Western larch: Average and standard deviation	Western larch: Trees
		- - - - - - Number - - - - - -		- - - - - - Number - - - - - -	
1980	Ashby	219 ± 318	206	147 ± 274	134
	Blue	46 ± 141	497	107 ± 238	192
	Lolo	187 ± 300	61	74 ± 271	132
	Spring	287 ± 428	58	159 ± 340	113
1981	Ashby	<1 ± <1	241	7 ± 16	167
	Blue	0 ± 0	600	1 ± 2	275
	Lolo	<1 ± 3	120	3 ± 12	291
	Spring	<1 ± <1	107	3 ± 12	163
1982	Ashby	8 ± 23	240	9 ± 19	167
	Blue	64 ± 99	590	31 ± 52	271
	Lolo	101 ± 82	82	19 ± 51	265
	Spring	20 ± 119	119	3 ± 11	168
1983	Ashby	<1 ± 1	144	21 ± 47	115
	Blue	<1 ± <1	621	10 ± 29	283
	Lolo	<1 ± <1	64	3 ± 10	206
	Spring	9 ± 25	119	10 ± 35	167

Production by Year

About 80 percent of all Douglas-fir and western larch cones counted during the 4 years of this study were produced in 1980. Twenty percent of the Douglas-fir cones were counted in 1982, and less than 1 percent in 1981 and 1983. Two, 11, and 7 percent of the larch cones were counted in 1981, 1982, and 1983.

The average number of cones per tree also varied each year by location (table 3). Greatest average cone maturity for the 4-year period occurred at Spring, where average basal area and crown competition were least. Lowest cone production occurred at Blue, where the highest basal area was measured. Although most of the Douglas-fir cones were produced in 1980, more cones matured at Blue in 1982 than in 1980 (table 3). This difference would have been even greater if insect-caused mortality of conelets in 1982 was kept at the same level as in 1980 (Shearer 1984). The low Douglas-fir cone counts in 1983 at Ashby and Blue resulted from high conelet mortality caused by insects.

Production by Diameter Class

More Douglas-fir and larch cones were produced on larger diameter trees, probably because of greater crown volume. In 1980, cone production at least tripled in each larger diameter class (table 4). This trend was similar at all locations, although the average number of cones varied from lower counts at Blue to higher counts at Spring. The number of Douglas-fir cones on each tree ranged from 0 to 698 in the 10- to 15-cm (4- to 6-inch) (small) diameter class, 44 to 1,065 in the 20- to 25-cm (8- to 10-inch) (mid) diameter class, and 81 to 1,482 in the 30- to 36-cm (12- to 14-inch) (large) diameter class. The number of western larch cones on each tree ranged from 0 to 750 within the small diameter class, 0 to 1,200 within the mid diameter class, and 0 to 2,450 within the large diameter class.

Cone production in 1981, 1982, and 1983 was much lower than in 1980. Nevertheless, the average number of Douglas-fir and western larch cones per tree increased in each larger diameter class except in 1981 when so few Douglas-fir cones were produced that the trend was not evident (table 4). One Douglas-fir at Lolo had 30 cones--the greatest number found in the four study areas. Most western larch also failed to produce cones in 1981 and the maximum number of cones was 85, 130, and 55 in the small, mid, and large diameter classes.

The number of Douglas-fir cones in 1982 ranged from 0 to 360 within the small, 0 to 550 within the mid, and 0 to 400 within the large diameter classes; larch cones ranged from 0 to 150 within the small, 0 to 250 within the mid, and 0 to 300 within the large diameter classes.

In 1983, cone production on Douglas-fir ranged from 0 to 66 within the small, 0 to 104 within the mid, and 0 to 176 within the large diameter classes. Larch cone production in 1983 ranged from 0 to 57 within the small, 0 to 117 within

Table 4.--Average number of Douglas-fir and western larch cones per tree and number of trees sampled each year by diameter class for four locations, western Montana

Year	Diameter class	Douglas-fir: Average and standard deviation	Douglas-fir: Trees	Western larch: Average and standard deviation	Western larch: Trees
	Inch	Number		Number	
1980	4- 6	41 ± 114	377	21 ± 79	261
	8-10	132 ± 232	366	116 ± 210	247
	12-14	434 ± 519	63	575 ± 536	55
1981	4- 6	<1 ± 1	509	1 ± 5	444
	8-10	<1 ± <1	464	4 ± 13	361
	12-14	0 ± 0	77	6 ± 12	78
1982	4- 6	17 ± 49	490	5 ± 16	434
	8-10	72 ± 99	450	26 ± 47	348
	12-14	122 ± 139	72	48 ± 78	76
1983	4- 6	<1 ± 4	434	1 ± 5	376
	8-10	1 ± 7	426	9 ± 17	319
	12-14	6 ± 26	70	56 ± 82	69

the mid, and 0 to 272 within the large diameter classes.

The percentage of trees that produced cones increased with size of cone crop:

Size of cone crop	Douglas-fir	Western larch
1 (largest)	49 (1980)	48 (1980)
2	43 (1982)	24 (1983)
3	2 (1983)	22 (1982)
4 (smallest)	<1 (1981)	13 (1981)

In 1981, of 1,050 Douglas-fir trees examined, only seven produced cones. In 1983, 2, <1, and 3 percent of the trees at Ashby, Blue, and Lolo produced cones. At Spring, however, 24 percent of the trees produced cones. The 1982 and 1983 larch cone crops had about half as many trees produce cones as in 1980. As more trees produced cones, the average number of cones per tree also increased.

The percentage of trees that had cones increased in the larger diameter classes. An average of only 13 percent of the larch in 1981 produced cones; in the small, mid, and large diameter classes, 5, 18, and 32 percent of the trees yielded cones (table 5). Cones were on 49 percent of the Douglas-fir and 48 percent of the larch in 1980. In Douglas-fir, 45, 60, and 86 percent of the small, mid, and large diameter classes produced cones (table 5). In western larch 38, 50, and 84 percent of the small, mid, and large diameter classes had cones. The Douglas-fir cone crop of 1982 matured cones on 22, 60, and 75 percent in the small, mid, and large diameter classes. The larch cone crops of 1982 and 1983 produced cones on an average of 12, 27, and 58 percent in the small, mid, and large diameter classes.

Table 5.--Percent of Douglas-fir and western larch in four western Montana study areas that had 0, 1-99, and more than 99 cones per tree each year by diameter class

Year	Diameter class	Douglas-fir 0	Douglas-fir 1-99	Douglas-fir >99	Western larch 0	Western larch 1-99	Western larch >99
1980	4- 6	55	33	12	62	35	3
	8-10	40	29	31	50	32	18
	12-14	14	22	64	16	14	70
1981	4- 6	100	0	0	95	5	0
	8-10	>99	<1	0	81	18	1
	12-14	100	0	0	68	32	0
1982	4- 6	78	16	6	84	15	1
	8-10	40	29	31	78	14	8
	12-14	25	35	40	48	29	23
1983	4- 6	98	2	0	91	9	0
	8-10	98	2	0	68	30	2
	12-14	95	2	3	36	42	22

The frequency of cone production varies by species (table 6). During these 4 years, larch had cones more frequently than Douglas-fir. Although 34 percent of the trees of both species failed to have any cones, 26 percent of the larch and only 1 percent of the Douglas-fir had

cones in 3 or in all 4 years. The remaining 40 percent of the larch and 65 percent of the Douglas-fir produced cones 1 or 2 of the 4 years.

Table 6.--Percent of Douglas-fir and western larch trees in four western Montana study areas that had one or more cones during the 4 years of the study by species and diameter class

Species	Diameter class	Number of years cones produced				
		0	1	2	3	4
Douglas-fir	4- 6	51	38	11	0	0
	8-10	24	35	40	1	0
	12-14	7	25	65	3	0
Western larch	4- 6	54	27	11	7	1
	8-10	22	17	24	27	10
	12-14	6	4	36	33	21

As the diameter increased, the frequency of cone production usually increased (table 6). For example, 11, 41, and 68 percent of the Douglas-fir and 19, 61, and 90 percent of the larch of the small, mid, and large diameter classes had cones 2, 3, or 4 years of the study. More than half of the Douglas-fir and larch trees in the small diameter class failed to produce cones any of the 4 years; less than one-fourth and one-tenth of the mid and large diameter classes failed to produce cones in any of the 4 years.

MANAGEMENT IMPLICATIONS

Although Douglas-fir produced more cones per tree than did western larch during the 4 years of this study, larch produced some cones every year; Douglas-fir nearly failed to produce cones in 2 of the years. Where seed production is an important consideration, larger diameter full-crown dominant and codominant Douglas-fir and western larch should be reserved because larger trees produce more cones more frequently than smaller diameter trees. The number of mature Douglas-fir cones tripled from the small to the mid diameter class and tripled again from the mid to the large diameter class. Western larch cones increased fivefold through each of the diameter class comparisons.

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CONE PRODUCTION IN PINUS ALBICAULIS FORESTS

T. Weaver and F. Forcella

ABSTRACT: Whitebark pine cone production was estimated for a 6 to 8 year period in each of 29 stands widespread in the northern Rocky Mountains. 1) One-time sampling was possible since the estimate was made by multiplying the number of branches per m^2 by an estimate of annual cone production made from counts of conelets, mature cones, or cone scars on successively older annual increments of those branches. 2) Average cone production ranged from 0.3 to 3.6 cones$\cdot m^{-2}\cdot yr^{-1}$ and from 22-270 seeds$\cdot m^{-2}\cdot year^{-1}$. 3) Regression analysis was used to relate the variance observed to time and place. a) Year-to-year variation in the cone yield of branches, trees, and stands in a region appears to be both internally and externally controlled. Internal control is suggested by the fact that good cone years were usually preceded by poor cone years. While external control is indicated by significant correlations between growth and weather conditions, control is not dominated by the effect of any one factor or any particular developmental stage. b) Although cone production of the average branch varied significantly within 30 percent of the trees and within 48 percent of the stands observed, it did not vary significantly among stands. c) Regressions relating stand cone production to easily measured stand characteristics such as canopy cover, fallen cones, and/or stand size explain no more than 50 percent of the variance among stands.

INTRODUCTION

Pinus albicaulis (whitebark pine) is a dominant or codominant tree in many high-altitude forests of western North America (Weaver and Dale 1974; Arno 1986). Its large, well-provisioned seeds are important not only for their reproductive function, but also as food for man, bears, squirrels, and nutcrackers (Blankenship 1905; Forcella and Weaver 1980; Kendall 1980b; Hutchins and Lanner 1982; Tombach 1983). Managers considering either of these functions might ask: What is average production? How does it vary between stands? How does it vary between years? And how might I estimate these variables in an unstudied stand?

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This paper (1) demonstrates a method for estimating a stand's cone production over a 6 to 8 year period after a single sampling, (2) reports estimates made in 29 stands widespread in the northern Rocky Mountains, and (3) uses that data set both to determine the relationship of yield to easily measured stand characteristics and to determine the relationship of yield to regional weather conditions.

METHODS

Cone production.--Cone production in the 1969 through 1976 period was estimated for 29 P. albicaulis stands from the Montana-Idaho border [Bitterroot (5 stands) and Salmon River (2) Mountains], from southwest Montana [Little Belt (1), Big Belt (3), Castle (3), Elkhorn (2), Pioneer (1), Tobacco Root (2), Madison (3), and Bridger Mountains (1)] and from western Wyoming [Absaroka (3), and Wind River Mountains (3)]. More exact locations are given by Forcella (1977).

The measurements necessary for these estimates were made as follows:

1. Current, future, and past production were determined for 25 representative shoots, that is five shoots each from the tops of five representative trees.

2. The number of shoots per m^2 in the canopy was determined by counting the potential cone bearing leaders on each of the five trees and dividing by a canopy area calculated from the tree's greatest and least canopy diameters.

3. Tree cover in the study area was determined as a percent of 90 overhead points covered by the canopy; the points were examined through a vertical periscope held at meter intervals along three 30 meter lines placed parallel to the slope at three representative sites in each stand studied.

Though our method has the advantage of allowing one to sample production over a series of years simultaneously, the following problems should be recognized:

1. The trees were not sampled randomly because some trees could not be climbed.

2. Shoots could not be sampled randomly because some were in inaccessible parts of the crown.

3. Heavy bearing shoots may have been absent or undersampled due to animal predation. Trees raided by black bears (Ursus americanus), recognizable by claw marks and broken branches, were therefore not sampled. Less easily avoided were the effects of red squirrels (Tamiasciurus hudsonicus) who commonly cut leader shoots from the trees (Schmidt and Shearer 1971).

4. On the other hand, shoots bearing cones at the time of sampling are also apparent to man and are likely to be over sampled; this may compensate for underestimation due to predation.

5. Estimates of the coming cone crop will be high if significant numbers of immature cones abort (compare with Allen 1941, Finnis 1953, and Sarvas 1962); cone numbers predicted for 1977 were not significantly higher than the actual crop--as they would have been if abortion had been significant.

A second measure of cone production was made by counting cones which fell to the ground in three 6.67 x 30 M plots in each stand. Estimates of the 1973 cone crop were made in 14 stands in 1974, estimates of the 1974 cone crop were made in 28 stands in 1975, and numbers of old weathered cones were recorded in both years.

Relating production to environment.--A nested analysis of variance was used to evaluate the effects of place and time on cone production. The analysis detailed below determined the significance ($p<0.05$) of variation between 5 branches in a tree, 5 trees in a stand, 6 to 16 stands in a floristically defined subassociation and 29 stands in the entire Pinus albicaulis-Vaccinium scoparium association. Annual variation in production was simultaneously tested as an interaction in each nest of the analysis. The three floristic regions included: 1. the Wind River and Absaroka Mountains; 2. central and southwestern Montana; 3. the Bitterroot and Salmon River Mountains (compare with Forcella 1977).

The significant effects of time detected in the preceding analysis were tentatively attributed to weather. To clarify the relationship between cone yield and weather we regressed deviations of normalized cone yields against deviations of weather variables (monthly mean temperature and monthly total precipitation) from their means in each of the 46 months preceding abscission (compare with Eis 1976). Cone yields were normalized to eliminate the effect of large differences in average yield between stands. Regional average weather data were used (USDC 1966-1976, compare with Lowry 1966) because no data are available from Pinus albicaulis stands, because deviations in precipitation or temperature from normal at low altitude usually parallel those found at high altitude, and because regional averages should eliminate weather station peculiarities like frost pockets. Each regional weather datum summarizes the data from dozens of official weather stations.

Relating production to simple stand parameters.--Simple or multiple regressions of cone production (leader number x average leader yield, table 1) against canopy cover, tree basal area, fallen cone number, and stand size explained significant amounts of the observed variation. On the other hand, regressions of cone yield against stand age, stand area, stand elevation, stand slope-aspect, total productivity, total standing crop, and cover indicator plants either alone or in combination were never significant.

RESULTS AND DISCUSSION

Cone development.--Cone history is reviewed here as a basis for understanding our method, for relating seed production to climatic factors, and as partial explanation for within-stand tree distribution. The development of Pinus albicaulis cones occupies parts of three summers and, due to apical branch growth, evidence of progressively older cones is displayed at nodes increasingly removed from the branch tip.

1. Late in the first summer a bud develops at the branch apex.

2. Pistillate conelets emerge from these buds in the second summer about the time of snowmelt (early July); they are found in the first lateral branch whorl, are purple, are about 5 mm long, and are easily recognized. July is therefore the best month to analyze shoots to predict the two forthcoming cone crops (compare with Allen 1941). Staminate strobili mature in early July and pollination occurs at this time. By the end of the growing season (mid-September) the conelets are approximately 1.5 cm long by 0.9 cm in diameter.

3. Rapid growth begins again in July of the third summer and full size (6.3 x 4.7 cm) cones appear in the second branch whorl by mid-August. Cone maturation continues until mid-September or early October when abscission normally occurs. Undisturbed cones abscise and fall to the ground intact, but if Clark's nutcracker (Nucifraga columbiana) removes the cone scales before abscission, the cone axes may remain in lower whorls of the branch for up to 10 years (compare with Smechkin 1963). Perhaps abscission depends on a hormone produced in the cone scales shortly before abscission so that if the cones are destroyed prior to its synthesis abscission does not occur.

The cones exude and are coated with a viscous aromatic resin. The resin may reduce seed predation by squirrels (Smith 1970) and nutcrackers. It also bonds the cone scales together (Clements 1910) until the resin crystallizes or is consumed by fungi. When the cone falls from the tree, cone scales and the large wingless seeds fall away from the axis; small clusters of seedlings found on the forest floor may result either from in situ disarticulation or from animal caches (compare with Hutchins and Lanner 1982).

Table 1.--Cone crops, locations, and stand characteristics for 28 *Pinus albicaulis* stands

STD[1]	MTN[2]	STATE[1]	CLIM[4]	COVER[5]	SIZE[6]	AGE[7]	1976	1975	1974	1973	1972	1971	1970	1969	MEAN+SE[8]
16	WR	WY	WR	63	2	198	2.7	2.5	0.3	2.5	1.0	2.5	--	--	1.9+0.4
17	WR	WY	WR	63	1	161	2.0	3.8	1.6	1.6	1.4	1.1	--	--	1.0+0.4
18	WR	WY	WR	71	1	214	1.3	1.3	0.7	0.8	0.6	1.5	--	--	1.0±0.2
19	AB	WY	WR	63	1	131	0.7	1.7	0.2	0.9	0.9	0.7	--	--	0.9±0.2
20	AB	MT	SC	49	1	210	1.2	1.9	1.7	0.7	0.6	1.3	--	--	1.2±0.2
09	AB	MT	SC	54	2	307	0.9	1.4	1.6	1.2	1.5	0.5	0.9	--	1.1±0.2
07	BB	MT	CN	61	2	120	0.0	0.1	9.0	3.1	3.7	3.9	1.7	3.5	3.1±1.0
06	BB	MT	CN	51	3	364	0.5	0.4	2.7	1.6	1.8	2.5	0.8	1.7	1.5±0.3
08	BB	MT	CN	66	3	55	1.7	0.4	2.6	0.2	0.2	1.5	0.2	1.9	1.1±0.3
03	LB	MT	CN	66	3	132	0.2	0.0	3.8	1.8	0.5	1.3	--	--	1.3+0.6
05	CA	MT	CN	70	1	330	0.9	0.0	1.8	0.6	0.9	0.8	--	--	0.8±0.2
05	CA	MT	CN	70	1	330	0.9	0.0	1.8	0.6	0.9	0.8	--	--	0.8±0.2
04	CA	MT	CN	37	2	55	1.5	0.3	1.2	0.7	0.2	0.6	--	--	0.8±0.2
10	MD	MT	SW	52	1	205	0.6	0.8	0.7	0.2	0.6	0.9	0.2	--	0.6±0.1
01	MD	MT	SW	73	2	150	0.6	3.8	1.2	2.2	0.9	1.8	0.9	--	1.6±0.5
02	MD	MT	SW	97	2	240	1.1	4.9	5.4	4.6	3.1	4.6	1.2	--	3.6±0.7
12	EH	MT	SW	73	2	135	1.5	6.1	1.9	2.2	2.0	3.9	1.4	4.2	2.9±0.6
11	EH	MT	SW	40	3	53	0.3	2.1	0.6	0.5	0.5	1.3	0.3	1.3	0.9±0.2
14	TR	MT	SW	56	2	160	1.5	3.6	3.3	0.5	2.7	3.8	0.5	--	2.3±0.5
13	TR	MT	SW	47	2	643	0.3	0.2	0.4	0.3	1.3	0.6	0.2	--	0.5±0.1
15	BR	MT	SW	53	2	320	1.0	0.0	1.2	0.0	0.1	0.1	--	--	0.4±0.2
29	PI	MT	SW	69	3	182	1.1	2.8	8.4	2.8	6.2	3.3	0.9	3.6	3.6±0.9
22	BT	MT	WE	50	2	423	2.5	1.1	44.9	2.3	2.4	2.7	1.2	1.0	2.3±0.4
23	BT	MT	WE	18	2	29	0.5	0.8	0.5	0.8	0.8	0.3	0.1	0.1	0.5±0.1
24	BT	MT	WE	13	1	32	0.7	0.2	0.3	0.3	0.3	0.3	0.0	0.1	0.3±0.1
25	BT	MT	WE	22	2	115	0.7	3.7	0.8	3.8	1.7	1.1	0.7	0.4	1.6±0.5
26	BT	ID	NV	32	2	59	0.1	2.3	0.3	1.0	1.2	0.6	0.2	0.4	0.8±0.3
27	SR	ID	NV	30	2	94	1.1	2.6	0.8	1.9	1.1	0.7	0.3	0.5	1.1±0.3
28	SR	ID	NV	31	2	188	0.1	0.9	0.4	0.6	0.4	0.2	0.1	0.2	0.4±0.1

1 Stand number.
2 Mountain ranges are: Absaroka(AB), Big Belts(BB), Bitterroot(BT), Bridger(BR), Castle(CA), Elkhorn(EH), Little Belts(LB), Madison (MD), Pioneer(PI), Salmon River(SR), Tabacco River(TR), and Wind River(WR).
3 States are: Idaho(ID), Montana(MT), and Wyoming(WY).
4 Climate regions are: Central(CN), Northeastern Valley(NV) of Idaho, South Central(SC), Southwest(SW), Western(WE) Montana, and Wind River(WR) Wyoming.
5 Tree canopy cover (percent).
6 Stand size where 1=0 to 0.75 ha, 2=0.75 to 1.25 ha, and 3=1.25 ha +.
7 Age of dominant trees.
8 Cones per square meter.

Cone-and-seed-production.--Average stand cone production ranged from 0.3 to 3.6 cones$\cdot$m$^{-2}\cdot$yr^{-1} and averaged 1.4 ± 0.2 cones$\cdot$m$^{-2}\cdot$yr^{-1} (table 1). Among the 6 to 8 years studied, maximum production in different stands ranged from 2.1 to over 100 times minimum production; in the median stand maximum production was 6.5 times minimum production (table 1). The average coefficient of variation (standard deviation/mean) between years in the average stand was 0.7.

The average mature pistillate cone weighed 23 ± 7 grams (range 10 to 50 gm) with cones produced in good years tending to be larger than those produced in poor years. Average cone production ranged, then, from a minimum of 7 to an average of 32 and to a maximum of 83 gm$\cdot$m$^{-2}\cdot$yr^{-1} on a ground area basis. The range observed across all years and stands was 0 to 193 gm$\cdot$m$^{-2}\cdot$yr^{-1}. Cone production was approximately 9 percent of total above- and belowground production in 14 stands in which total production was measured (Forcella and Weaver 1977).

The numbers of cones found on the ground were usually fewer than scars counted in tree tops. This relationship is demonstrated by the regression equation:

$$C = 0.305 + 1.314 F$$

where C = the number of 1974 cone scars counted in the treetop, F = the number of fresh cones counted on the ground in 1975, and $r^2 = 0.51$. Smechkin (1963) compared similar methods in a *Pinus sibirica* forest with the same result (r^2=0.62).

Table 2.--Comparison of cone and seed crops of several Pinus forest types[1]

Forest Type	Average Cones $\cdot m^{-2} \cdot yr^{-1}$			Average Seeds $\cdot m^{-2} \cdot yr^{-1}$			Reference
	#	grams	%[3]	#	grams	#[4]	
Pinus contorta	4.7	28	--	268	0.6	2	Smith 1968, 1970
P. contorta-Purshia tridentata	4.8	24	--	120	0.4	2	Lotan 1967
P. contorta-Geranium fremontii	8.0	40	13	---	---	-	Moir 1972
P. contorta-Vaccinium myrtillus	8.0	40	5	---	---	-	Moir 1972
P. cortorta bolanderi	---	52	20	---	---	-	Westman and Whittaker 1975
P. sibirica	---	--	--	100	30	-	Formosof 1933
P. sibirica-Vaccinium myrtillus	0.1-2.4	--	--	---	---	-	Boichenko 1970
P. sylvestris-Calluna vulgaris	1.5	9	--	30	0.2	2	Sarvas 1962
P. sylvestris-Vaccinium myrtillus	3.0	18	--	60	0.4	2	Sarvas 1962
P. sylvestris-Oxalis acetosella	4.5	27	--	90	0.6	2	Sarvas 1962
P. monophylla-Juniperus osteosperma	0.1-1.8	2-34	--	1-26	1-9	28	Forcella unpubl.
P. edulis-Juniperus osteosperma	0.8	--	--	8	---	-	Forcella unpubl.
P. cembroides-Juniperus deppeanna	7.3	17	--	35	6	35	Forcella unpubl.
P. albicaulis-Vaccinium scoparium	0.3-3.6	6-84	10	20-250	2-25	30	Forcella and Weaver 1977

1 Masses of seeds and cones not provided by the author were taken from Schopmeyer (1974).

2 Ranges in figures represent smallest and largest data provided.

3 Percent total productivity except third and fourth forest types which are percent aboveground productivity only.

4 Percent total cone mass.

We attribute the deficiency of cones found on the ground (about 25 percent) to Clark's nutcracker, squirrel, and bear activity.

Typical cones contain about 75 ± 28 seeds, each weighing 0.1 ± 0.02 gm dry. Seed live weights are about 0.17 gm (Schopmeyer 1974). Seed mass usually comprises 30 percent of cone mass and may comprise 50 percent in an especially good cone year; the proportion of cone mass devoted to seeds in other conifers is usually lower (Smith 1970 and table 2). Average seed production ranged, then, from a minimum of 2.3 to an average of 10.5 to a maximum of 27 $gm \cdot m^{-2} \cdot yr^{-1}$, i.e., from 23 to 105 to 270 $seeds \cdot m^{-2} \cdot yr^{-1}$. The range observed across all years and stands was 0-63 $gm \cdot m^{-2} \cdot yr^{-1}$ and 0-630 $seeds \cdot m^{-2} \cdot yr^{-1}$. Seed production was about 3 percent of total arboreal production in 14 stands studied intensively (Forcella and Weaver 1977a). Of the approximately 75 scales on a typical cone, one third, mostly apical and basal scales, were infertile.

Comparison of Pinus albicaulis forests with other pine forests (table 2), leads to the following conclusions: Pinus albicaulis forests produce normal cone crops (32 $gm \cdot m^{-2} \cdot yr^{-1}$ average). Because the cones are heavy, cone numbers are relatively small (1.4 $cones \cdot m^{-2} \cdot yr^{-1}$ average). Since a large proportion of the cone is devoted to seed, seed production is relatively high (10 $gm \cdot m^{-2} \cdot yr^{-1}$ average), yet because the seeds are large, seed numbers are normal (105 $m^{-2} \cdot yr^{-1}$ average). The net effect is to deposit normal numbers of abnormally well provisioned seeds.

Variation in cone production potential.--Total cone production is the product of mean shoot production (=cone production potential) multiplied by the number of fertile shoots per hectare. Yet, since the density of fertile shoots in a stand may be less than optimal, the yield of the average fertile shoot may be a better index of site production potential than is the total number of

cones actually produced in the stand. In the following discussion we therefore compare production potentials across vegetational units of increasing size (trees, stands, sub-association, and the entire association) by considering a sample of branches of fixed size and ignoring the actual number of shoots producing cones.

Cone crops varied significantly between branches in 29 percent of the trees studied, and between trees in 48 percent of the stands studied, but they did not vary significantly between stands in any region or between stands in all the different regions. One might conclude:

1. that cone production varies little between branches of a tree due to identical genetics and similar mesoenvironmental conditions,

2. that it varies more between trees in a stand due to greater dissimilarity in genetics and mesoenvironmental conditions, and

3. that it differs relatively little between stands in a region due to averaging of between-tree heterogeneity in forests with relatively constant genetic and mesoenvironmental conditions.

The fact that fertile branches have similar cone production potentials throughout a region or even throughout an association supports our expectation that the average cone production of a stand is determined primarily by the number of fertile shoots per hectare and their interaction with weather conditions.

Variability in time.--In the analysis of cone production potential just discussed, the between-year effect was tested as an interaction at each level. Branch production, tree production, and stand production varied significantly between years ($p=0.05$) in 60 percent, 78 percent, and 100 percent of the cases, respectively. When all stands in the three regions were considered simultaneously there were no significant differences between years.

Variability of production in time is apparently due, in part, to internal factors. Excellent cone years (with yields one standard deviation or more above mean yield) were preceded in 20 of 29 cases by poor cone years (with yields equal to or less than the mean). Since the probability of a poor seed year so defined is 50 percent, this is a significant deviation (<0.05) from our expectation. In other species poor fruit years are also followed by good fruit years, apparently because initiating fruits cannot compete with maturing fruit for available carbohydrates during initiation and development (Kozlowski 1971). The amplitude of natural cycles in fruiting might be increased by natural selection if poor seed years preceding excellent seed years resulted in better establishment of the tree through temporarily overprovisioning previously starved-out predator populations (compare with Janzen 1971, Forcella 1980); such selection could occur only if the seed predator used the subject as its principle source of food. Other variations may not have internal causes. For example, we see no physiological or evolutionary reason for the fact that 16 of 21 excellent cone crops were preceded 4 years earlier by a poor cone year ($p<0.05$).

Especially poor cone years (with yields more than one standard deviation below the mean) were not significantly correlated with yields in any previous year; we therefore think a poor cone year is more likely determined by weather rather than by internal factors.

We hypothesized that the demonstrated synchrony of variation in cone production within a stand and within a region is due to weather; and similarly, that the lack of synchrony between regions is due to differences in weather between regions. To clarify the relationship between cone yield and weather we regressed deviations of normalized cone yields against deviations of weather parameters (mean temperature and total precipitation) from their means in each of the 46 months preceding cone abscission as explained under methods (compare with Eis, 1976).

Cone production was correlated with preceding weather conditions, but in no simple way (table 3); six observations follow:

1. In well-sampled regions (represented by six to eight stands) correlations with temperature or rainfall significant at the 0.05 level may occur in half and correlations significant at the 0.001 level may occur in 20 percent of the 46 months preceding cone maturation. While significant correlations become progressively harder to detect as sample sizes decrease to two stands per climatic region, it might be possible to detect significant correlations in every month if sample sizes were increased sufficiently.

2. Though many correlations are highly significant, few explain much of the observed variation in cone yield. The average r^2 is 0.21 for precipitation and 0.20 for temperature and the r^2 of correlations significant at the 0.001 level are only 0.30 for precipitation and 0.35 for temperature. Assuming that variation in regional data parallels variation in higher altitude conditions, this suggests that each of the 46 months preceding cone abscission plays a small but important part in determining yield. If final yields of P. albicaulis are, in fact, determined by a summation of everyday conditions, unique events are notably less important to yields than they are for pinyon pine (Forcella 1981).

3. Numbers of significant correlations for both temperature and precipitation are similar in the prebud, bud, pollination, and cone maturation years.

4. Forty-five percent of the significant temperature correlations and 48 percent of the significant precipitation correlations occurred in winter months (November-April) when 'inactive'

Table 3.--Statistically significant relationships of cone yield to weather of the 46 months preceding cone drop in southwest Montana[1]. Correlation coefficients are presented with their signs; regressions significant at the 0.1 percent, 1 percent, and 5 percent level are indicated by a, b, and no letter respectively

Factor	Temperature				Precipitation			
Year[2]	preb	bud	juv	mat	preb	bud	juv	mat
JAN	-29				+40b		-51a	+34b
FEB		-32	+43a	+42b	-40b		-35b	+48a
MAR	+39b				-45a		+54a	
APR						+29	-31	
MAY		+45a	-30	-37b		-36b		
JUN			+50a	-26		+32	-49a	
JUL	-40b				-33			
AUG		+33			+46a	-40b		
SEP	-26							-56a
OCT			+41b		-32	+31	-31	+46a
NOV			+41b		-32	+31	-31	+46a
DEC		+32			-48a		+27	

1 Normalized deviation of yield was regressed against deviation from average climatic data as explained in the text. Correlations for other regions were generally of similar size, sign and significance and generally showed similar seasonal distribution. They will be provided upon request.

2 Years are those before bud formation (preb), of cone bud formation (bud), of juvenile pollinated cones (juv), and of cone maturation (mat).

trees might be assumed to be little affected. Correlations with winter precipitation could be due to its effect on summer soil water supply. The remaining significant temperature correlations were 20 percent in spring (May-June), 16 percent in summer (July-August) and 19 percent in fall (September-October). The remaining significant precipitation correlations were 15 percent in spring, 18 percent in summer, and 19 percent in fall.

5. Negative correlations are slightly more common than positive correlations between cone yields and summer (80 percent negative in July-August) and winter (57 percent negative in November-April) temperatures, as they are with spring (70 percent negative in May-June), fall (65 percent negative in September-October), and winter (62 percent negative in November-April) precipitation. We are not ready to conclude that high temperatures and heavy precipitation lower yields.

6. The fact that highly significant correlations between yield and a given developmental period may differ in sign between different areas is consistent with the observation that year-to-year variability in cone production disappears when one averages across regions.

Our results will frustrate anyone wishing to predict future cone crops from weather data. The highly significant, but weak, correlations observed suggest that a complex physiological model would be needed to make such predictions and that its final prediction wouldn't be available until shortly before the crop matured. Similar results could be had by sampling branches in a specific stand for numbers of mature or juvenile cones and, since stands in a region behave similarly, results from a representative stand might predict regional crops reasonably.

Variability associated with easily measured stand characteristics.--The considerable variability of average cone production among stands must be caused directly by site characteristics such as climate and soils and stand characteristics such

Table 4.--Regressions relating cone production[1] to easily measured stand characteristics[2]

Regression equations.	r^2
C_a = 0.470 + 0.00032 canopy cover^2	0.42
C_a = 0.288 + 0.023 basal area	0.28
C_a = 0.812 + 0.439 fallen cones	0.32
C_a = 0.450 + 0.00023 canopy cover^2 + 0.206 fallen cones	0.46
C_a = 0.430 + 0.00032 canopy cover^2 + 0.470 stand size	0.52
C_g = 0.515 + 0.00039 canopy cover^2 + 0.734 stand size	0.49
C_p = 0.269 + 0.00011 canopy cover^2 + 0.001 stand size	0.32

[1] Cone production in the average year (C_a) is expressed as cones$\cdot m^{-2}\cdot yr^{-1}$. C_g and C_p represent cone production in good and poor years respectively.

[2] Units were percent of ground area for canopy cover, m^2/ha for basal area, and new plus old cones/m^2 on the ground for fallen cones. Stand size was scaled with 1 = 0 = 0.75 ha, 2 = 0.75 to 1.25 ha, and 3 = more than 1.25 ha.

as age, density, and the genetic allocation of photosynthate to reproduction. Few of these variables were studied because their measurement was too costly, time consuming, or difficult. On the other hand, correlations of average cone production with easily measured stand characteristics were tested because any strong correlations discovered would be useful for managers who wish to predict production in particular stands.

Measures of stand cover and fallen cones should be correlated with cone production since they index numbers of potentially fruiting branches and their previous fruitfulness (table 4). Canopy cover alone explained 42 percent of observed variation in cone production. Basal area only explained 23 percent of the variance, probably because branch numbers were more closely related to tree cover or circumference than cross-sectional areas. Perhaps due to uneven consumption by animals, numbers of fallen cones explained only 32 percent of the observed variation. A regression combining canopy cover and numbers of fallen cones was our second best (r^2=0.46).

Our best simple predictor of cone production (table 4, r^2=0.52) involved stand size with canopy cover. Besides explaining observed variation best, this estimator has the advantage of being least expensive to apply--both canopy cover and stand size can be estimated from aerial photos in the non-field season. The 'small stand effect' is likely due to poorer fertilization in small stands than in large ones; Sarvas (1962) observed poor pollination in Pinus sylvestris when stands were smaller than 2 ha. The fact that yields of cones in good cone years (C_g=yields greater than median yields) seem to be more affected by stand size than yields in poor cone years (C_p=yields less than in median years) suggests that other factors (probably weather), override the pollination effect in poor cone years.

Other potential estimators of stand production studied were less useful. Regression of yield against stand age, stand area, stand elevation, stand slope-aspect, productivity, biomass, and the cover of indicator plants alone showed no significant correlations. Complex combinations of these factors in multiple regressions increased attributal variability (r^2) to 60 percent but since these regressions are biologically uninterpretable they are not reported.

SUMMARY AND CONCLUSIONS

Evidence of cone production--juvenile cones, mature cones, or cone scars--located at progressively older nodes of terminal branches can be used to estimate cone yields of a branch over a 6 to 8 year period from a single observation. The product of mean branch yields, so determined, and fruiting branch density (branches per m^2) provides a measure of stand cone yield through the same period.

Average reproductive production in the 29 stands observed ranged from 0.3 to 3.6 cones$\cdot m^{-2}\cdot yr^{-1}$ and 23 to 270 seeds$\cdot m^{-2}\cdot yr^{-1}$. The coefficient of variation (SD/mean) between years for cone production in the average stand was 0.7 cones$\cdot m^{-2}\cdot yr^{-1}$. While seed numbers are comparable to those observed in other pine forests their weights were greater. Cone production comprised about 9 percent of total arboreal production.

Cone yield potentials varied significantly between branches in 30 percent of the trees studied and between trees in 48 percent of the stands studied, but never between stands.

Cone yields varied significantly between years in branches, trees, and stands in a region. Some internal control is suggested by the fact that high-yield years usually followed low-yield years. External control is indicated by significant correlations between regional weather and cone production. These correlations suggest that temperature and precipitation conditions have significant, but not dominant, effects in prebud, bud, juvenile cone, and mature cone years and all months of the year. Unique events seem less significant, therefore, for Pinus albicaulis than for Pinus edulis (Forcella 1981).

Easily measured stand characteristics are never more than mediocre predictors of average cone production. Our best regressions were based on canopy cover, canopy cover with fallen cones, and canopy cover with stand size. They explained 42, 46, and 52 percent, respectively, of the observed variation. Fortunately, the best predictor is also least expensive to apply.

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Section 2. Cone Prediction, Collection, and Processing

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CONE PREDICTION, COLLECTION, AND PROCESSING

D.G.W. Edwards

ABSTRACT: Methods of predicting the size of a cone crop and the seed yield are reviewed. The planning and methods of harvesting the crop, and the procedures for seed extraction, seed cleaning and sorting are discussed.

INTRODUCTION

The expansion of reforestation programs has created a greater focus on the problems of seed supply, particularly for specific provenances and for genetically improved seeds. Rising costs for all types of seedling production have emphasized the need for high-quality seeds.

Seed production in most conifers is periodic and intervals between good crops vary. In the years between heavy crops, few or no cones may be produced. So that seeds will always be available for forest regeneration, the forester must be able to predict a heavy crop, and must know how and when to harvest the seeds and how they must be processed. Where natural regeneration is planned, advance knowledge of a heavy crop allows for modification and timing of the logging methods, or site preparation, so that the approaching seed fall is used to the best advantage.

This paper provides a broad review of cone crop prediction, cone collection and seed processing. Crop prediction, or forecasting, is the means whereby the forest manager looks ahead, sometimes as much as one and a half years, for early signs that collectable quantities of cones may develop. Should the signals be positive, resources such as manpower, equipment and funding can be organized well ahead of the collection date. Since most conifer seeds ripen and begin to disperse in a relatively short period of time, cone collections must be carefully timed. Optimally, seeds should be mature, or nearly so, and free from insect or disease damage. Several methods of cone collection, some of them mechanized, have been developed and the most appropriate one must be chosen to suit the species, and stand and crop conditions. Cone and seed processing involves numerous steps that begin with seed extraction from dried, opened cones. In many species the seed wing must be removed before the seeds are cleaned of non-seed debris and impurities and sorted to remove empty or damaged seeds. Seedlot quality has to be checked in germination tests so that efficient use can be made of the seeds in the nursery, and the seeds have to be prepared and packaged for cold storage. While the concepts and methodology discussed relate principally to natural stands since these satisfy the bulk of reforestation needs both at present and for the immediate future, they can also be applied in seed orchards.

CONE CROP PREDICTION

Accurate crop predicting (or forecasting) is difficult since many factors affect the crop from its initiation to seed maturation, and these are incompletely understood. Successful predictions are based on knowledge of the reproductive cycles of the various species which have been described in detail for _Pseudotsuga menziesii_ (Mirb.) Franco, _Tsuga heterophylla_ (Raf.) Sarg., _T. mertensiana_ (Bong.) Carr., _Pinus contorta_ (Dougl.), _Thuja plicata_ Donn., _Chamaecyparis nootkatensis_ (D. Don.) Spach, _Picea engelmannii_ (Parry) and _P. glauca_ (Moench) Voss (Allen and Owens 1972; Owens 1973; Owens and Molder 1984a, 1984b, 1984c, 1984d). Predictions can be made at three main stages in the reproductive cycle: (i) the crop year before flowering, (ii) the early spring of the crop year and (iii) after flowering, when conelets are visible.

1. Predictions In The Crop Year Before Flowering

Early predictions are the most complex, since they are based on factors influencing the initiation of reproductive structures and their development. They are also the least reliable because many factors can subsequently damage the crop, so such forecasts need periodic revision and adjustment. Such predictions are based on observations on the periodicity (frequency) of cone crops over many years, the relationships to weather conditions preceding the crops, and the formation of reproductive stuctures in winter buds.

Periodicity.--The period between good seed crops varies within and among species (table 1). The phenomenon of alternate bearing is due to the developing crop having a negative effect on the subsequent year's crop. The reasons can be morphological as, for example, in _Picea glauca_, _Tsuga heterophylla_, _Thuja plicata_ and other trees that bear reproductive structures in terminal positions on the shoots, since these species do

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not have as many available locations for flower production the year following a good crop. Thus heavy crops are followed by light ones. The effects can also be physiological, the presence of a crop in one year influencing the initiation or development of buds the following year. In species that produce flowers on the previous year's shoots, such as Abies balsamea (L.) Mill. (Morris 1951; Powell 1977) or Pseudotsuga menziesii (Owens 1969; Allen and Owens 1972), new shoots tend to be short and few flower bud primordia develop, possibly because of a lower level of available carbohydrates during the year of a heavy crop. Lee and others (1979) concluded that a high carbohydrate: nitrogen ratio favored female strobilus initiation in Pinus elliottii Engelm. The minimum period between good crops in these and several other species is therefore two years (Morris 1951; Baron 1969; Dobbs and others 1976; Powell 1977). There is also some evidence that a maturing cone crop has an effect on future crops in species with a three-year reproductive cycle, such as some pines (Wenger 1957; Lester 1967; Baron 1969; Eis 1976) either by influencing the initiation and development of reproductive primordia or by affecting the developing conelets.

A heavy current crop, therefore, can be used in many species as an indicator that the next crop will be poor. However, instances of consecutive good cone crops have been reported in a number of species (Haig and others 1941; Fowells and Schubert 1956; Maguire 1956; Eis and others 1965; Lowry 1966; Franklin 1968; Rehfeldt and others 1971), although they are rare. In any year, wide differences in crop size between stands of the same species within a region may occur. Such events demonstrate that environmental factors may at times override the negative effects of previous seed production.

Table 1.--Periodicity in some western conifer species. (Source: Schopmeyer 1974)

Species	Interval between good crops (years)
Abies amabilis	2-3
Abies grandis	2-3
Abies lasiocarpa	2-4
Juniperus communis	irregular
Juniperus occidentalis	--
Juniperus scopulorum	2-5
Larix laricina	3-6
Larix lyallii	1-10
Larix occidentalis	1-10
Picea engelmannii	2-3
Picea glauca	2-6+
Picea mariana	4
Picea pungens	1-3
Pinus banksiana	3-4
Pinus contorta	1
Pinus flexilis	2-4
Pinus monticola	3-7
Pinus ponderosa	2-5
Pseudotsuga menziesii	2-11
Thuja plicata	3-4
Tsuga heterophylla	2-8
Tsuga mertensiana	1-5

In any given year the level of seed production may vary from one species to the next, and may vary from one region to another as well as among stands within a region (Haig and others 1941; McWilliams 1950; Rowe 1955; Waldron 1965b; Franklin 1968; Bingham and Rehfeldt 1970). Within a species, Franklin (1968) observed that stand to stand variation was least in heavy or very light crop years, and greatest when cone crops were medium.

Among pines, most species flower every year, yet some species are strongly cyclic in seed production (Wright 1953; Fowells and Schubert 1956; Maguire 1956; Lester 1967; Franklin 1968; Bramlett 1972). The main reason appears to be conelet abortion which can account for between 40% and 70% of the loss of a potential crop (Wright 1953; Sarvas 1962; Snyder and Squillace 1966; Lester 1967; Wang 1970; Shearer and Schmidt 1971; Bramlett 1972). High conelet loss has been related to low temperature at the time of pollination failure (Wright 1953; Sarvas 1962; Hard 1963; Boyer 1974; Schoenike 1955), physiological causes (Wright 1953; Sarvas 1962; Wang 1970; White and others 1977) and insect damage by feeding (DeBarr and Ebel 1974; Kormanik 1974; DeBarr and Kormanik 1975; Neel and others 1979).

Weather conditions.--In different species and climatic regions initiation and development of reproductive primordia occur at different times of the growing season (Gifford and Mirov 1960; Allen and Owens 1972). This is when weather conditions have been shown to be most critical. However, in many studies correlations have been found only when the weather has had a profound negative influence on the reproductive cycle so the use of climatic conditions in forecasting may only be of use when records of previous cone crops are considered (Calvert 1979). During primordia initiation and development (i.e., during the year preceding pollination) positive responses to warm, sunny weather have been noted (Lester 1967; Rehfeldt and others 1971; Eis 1973a, 1976) in many species with a two-year reproductive cycle (table 2). Moisture deficit during this period was linked by Ebell (1967) to increased strobilus production in Pseudotsuga menziesii.

In pines, interpretation of climatic effects on seed production is complicated by the three-year reproductive cycle and interactions with physiological factors causing primordia or conelet abortion (Calvert 1979). Positive correlations with weather patterns occur in several species (table 3) but only in Pinus monticola Dougl.

Table 2.--Species in which seed production increases following a warm, sunny summer

Species	Source (Period of Observation - years)
Abies grandis	Eis 1973a (37)
Abies sibirica	Miscenko 1963 (cited by Calvert 1979)
Larix leptolepis	Yanagihara and others 1960 (49) (cited by Calvert 1979)
Picea abies	LaBastide and van Vredenburch 1970 (38)
Picea glauca	Fraser 1958 (3)
Picea mariana	Fraser 1958 (3)
Picea omorika	Maurin and others 1970
Pseudotsuga menziesii	Eis 1973a (37) LaBastide and van Vredenburch 1970 (38) Lowry 1966 (48)
Tsuga canadensis	Maurin and others 1970

have correlations been found during the critical year of primordia initiation and the conelet and crop years.

Winter buds.--Interaction between climate and physiological processes becomes evident in the number of reproductive buds in species with a two-year cycle, or in the number of conelets in pines in the fall and winter preceding cone maturity. Numbers of male buds are closely correlated with the abundance of female buds in *Pseudotsuga menziesii* (Silen 1967) and *Pinus ponderosa* Laws. (Roeser 1941) and a crop prediction method based on male buds was proposed by Silen (1967). This relationship does not hold in other species (Wright 1953; Eis and Inkster 1972). Predictions are most frequently based solely on female bud abundance, using regression techniques (Medvedev and Pal'gov 1971), sequential sampling schemes (Roe 1966; Eis and Inkster 1972; Eis 1973b), or ratios of female to vegetative buds (Allen 1941a). The accuracy of these prediction methods has varied from species to species (Eis and Inkster 1972). Poor or nil crops can be predicted with 100% accuracy while forecasting of heavy crops may only be 70%-90% accurate. In pines, surviving conelets at the beginning of the second year may be used for crop predictions (Snyder and Squillace 1966; Shearer and Schmidt 1971) provided the size of the current cone crop is considered.

The use of reproductive buds in seed crop forecasting is a more direct and reliable approach

Table 3.--Positive correlations between weather and cone production in pines

Weather variable	Species	Source (Period of observation-years)
Year of primordia initiation:		
warm spring	Pinus banksiana	Larson 1961
	Pinus ponderosa	Maguire 1956 (23)
	Pinus resinosa	Lester 1967 (15)
warm, possibly droughty summer	Pinus monticola	Eis 1976 (20) Rehfeldt and others 1971 (18)
	Pinus ponderosa	Daubenmire 1960
	Pinus resinosa	Lester 1967 (15)
	Pinus sylvestris	LaBastide and van Vredenburch 1970 (38)
warm, possibly wet fall	Pinus monticola	Eis 1976 (20) Rehfeldt and others 1971 (18)
Year of conelets:		
rain following pollination	Pinus monticola	Eis 1976 (20)
warm fall	Pinus monticola	Eis 1976 (20)
Crop year:		
warm dry spring	Pinus monticola	Eis 1976 (20)

when bud types can be positively identified (Eis 1967; Eis and Inkster 1972). Cone crop prediction based on winter bud counts is the method now used in British Columbia since detailed, illustrated descriptions of reproductive bud and cone development have been published (Canadian Forestry Service 1983) for 18 western conifers. However, counting of buds still presents practical problems since representative twigs from the upper part of the crown must be sampled (Finnis 1953). These may be obtained by climbing, by shooting off the ends of branches using a rifle, or removal from recently felled trees. In some circumstances, sampling by helicopter may be justified. Samples are more readily obtained from seed orchards. Bud examinations can be carried out in the field or in the laboratory. In addition to these detailed examinations, shoots placed in containers of water can be "forced" (i.e., the buds will continue to develop and burst to reveal whether they are male, female or vegetative) under warm, humid well-lighted conditions. This process may require two to three weeks but it will confirm any diagnosis based on bud morphology.

Reproductive bud identifications, or conelet counts in pines, are carried out far enough in advance of a developing crop to provide the forester or seed orchard manager ample time to plan for a large collection operation if a heavy crop is indicated. But there is still time for the crop to fail, so its development during the spring and summer of the crop year should be monitored. However, if winter bud appraisals indicate a poor or nil crop, further preparations are unnecessary.

2. Predictions in Early Spring of the Crop Year

During the spring of the year in which the seed crop will mature, pollination and fertilization occur in species with a two-year reproductive cycle, while fertilization only takes place in pines. After bud burst, potential seed crops can be estimated from the abundance of developing strobili (Allen 1941a; Silen 1967; Eis and Inkster 1972). Usually, abundant megastrobili indicate a large seed crop, even in some pines (Lester 1967; Shearer and Schmidt 1971) but weather conditions before, during and after bud break may cause major losses (Wright 1953; Matthews 1963).

Date of flowering varies from species to species (Wright 1953; Ahlgren 1957; Boyer 1978) but since the relative order of flowering is usually the same from year to year (Wright 1953), poor weather will not necessarily affect all species. Strobilus development can be seriously disrupted by cold, or unusually dry weather at the time of bud burst, and megastrobili are particularly susceptible to frost damage during the receptive stage (Roeser 1942; Wright 1953; Barras and Norris 1964; Bramlett 1972; Eis and Inkster 1972; Timmis 1977). Environmental stresses during the pollination and fertilization sequences are major contributors to seed crop periodicity in many trees (Haig and others 1941). Cold weather may cause pollen cone drop in _Picea abies_ (L.) Karst (Sarvas 1968) and _P. glauca_ (Zasada 1971) and, in addition to or combined with moisture stress, has been known to arrest pollen development completely in _Pseudotsuga menziesii_ (Chira 1967). Since vegetative buds and shoots are less sensitive than reproductive structures to low temperatures (Hard 1963: Zasada 1971) strobilus damage may be overlooked unless the reproductive structures themselves are examined. Rain has damaged the quantity and viability of pollen in _Picea glauca_ (Nienstaedt 1958) and _Pinus ponderosa_ (Turner 1956). In contrast, wet weather has been reported to have no effect on the pollen of _Pinus sylvestris_ L. or _Pseudotsuga menziesii_ in other studies (Sarvas 1962; Silen 1962).

Methods of prediction based on strobilus abundance include regression techniques or sequential sampling, similar to those based on reproductive buds.

3. Predictions After Flowering

Predictions of the seed crop when the developing cones are visible on the trees are the easiest to use and the most accurate. Such surveys are the preferred method of crop forecasting in Ontario (Ontario Ministry of Natural Resources 1984). These forecasts not only consider the relative abundance of maturing cones, but they also take into account the quantity and quality of seeds. They allow minimum time for organization, however.

Cone crop rating.--Most rating methods are quantitative and are intended to indicate where crops are heaviest and if they are worth collecting. One method, devised for California conifers by Baron (1963) used five ratings against which crops were compared (table 4). This was based on a system described by Fowells and Schubert (1956) whose rating classes used actual numbers of cones, the numbers varying with the species. Unfortunately, Baron introduced the terms "light," "medium" and "heavy" making the method entirely

Table 4.--Cone crop rating system for California conifers (Source: Baron 1963)

Rating Category[1/]	Definition
1 -- None	- no cones on any trees
2 -- Very light	- few cones on less than 25% of the trees
3 -- Light	- few cones on more than 25% of the trees
4 -- Medium	- many cones on 25% to 50% of the trees
5 -- Heavy	- many cones on more than 50% of the trees

1/ Cones on full-crowned trees over 30 cm d.b.h.

subjective. For example, a given number of cones, say 80-100, on Pinus monticola would probably be categorized as "many" and might indicate a heavy crop, while the same number of cones on a mature Picea glauca or Pseudotsuga menziesii tree might go unnoticed. By the same token, a thousand cones on Picea engelmanii (Parry) Engelm. might constitute "many" but would be classified as "few" on a mature Thuja plicata (Dobbs and others 1976). "Medium" and "heavy" crops (table 4, categories 4 and 5) are generally considered collectable. Despite the subjectivity, similar systems have been applied elsewhere. A method using seven rating categories is used in British Columbia, while ten rating categories are used in Alaska (Zasada and Viereck 1970) as well as in Arizona and New Mexico (Schubert and Pitcher 1973). When rating a crop, attention has to be confined to that portion of the crown expected to bear cones. In Pinus monticola and Abies spp. this is limited to the top four or five whorls of branches, whereas in Picea glauca/engelmanii and Pseudotsuga menziesii the upper two-thirds of the crown is potentially cone bearing; in Thuja plicata and Pinus contorta cones may be found over the entire crown.

Other methods based on total cone counts, as well as that of Fowells and Schubert (1956), have been developed (Haig and others 1941; Wright 1953; Franklin 1968). In most species, especially those that bear crops over a large portion of the crown, such indices are limited in value, because cone production per tree increases with age, tree diameter and crown size (Haig and others 1941; Garman 1951; Crossley 1956; Roe 1963; Waldron 1965; Lotan and Jensen 1970; Stiell 1971). They may be used, however, to estimate cone yield to determine if a collection quota can be met. One exception is Pinus strobus L. which, past a certain size, does not increase its cone bearing crown with tree size so relatively small trees produce the same crop as larger ones (Wright 1953) except at high stand densities (Garber 1970).

Waldron (1965) used a subjective cone abundance rating which was then multiplied by an estimate of the surface area of the cone bearing portion of the crown to give a cone production index in Picea glauca. In Great Britain, Seal and others (1962) recommended that for Abies spp., Pseudotsuga menziesii, Picea sitchensis (Bong.) Carr. and Pinus sylvestris, the cones visible through 6x or 8x binoculars from a distance roughly equal to the tree's height can be counted and multiplied by four to estimate the total cones on the tree. Winjum and Johnson (1962) preferred to view a Pseudotsuga menziesii tree from its south side and to count the number of cones on one branch in each whorl. The total number of cones on the tree was estimated from a mathematical equation. A more complex method was proposed by Lotan and Jensen (1970) who used regression equations involving diameter at breast height, live crown ratio, stump height, age and partial cone counts in Pinus contorta. Diameter and age were found to influence cone production in Pinus ponderosa and Pseudotsuga menziesii by Linhart and others (1979). Relationships between seed production and basal area have been found in Picea engelmannii (Roe 1967), Pinus resinosa Ait. (Roe 1964; Stiell 1971), P. palustris Mill. (Crocker 1973) and P. strobus (Garber 1970).

The most useful quantitative rating methods are based on percentages of full crop values. These methods were first described for use with broad-leaved species (Sharp 1958; Grisez 1975). They compare current fruit counts with the maximum counts ever made, and offer promise in making estimates from different sources comparable. Although they have application in research (Calvert 1979), they require more effort to apply than qualitative systems and may not be much more advantageous for large-scale predictions.

Two common errors made in rating cone crops are counting old cones that have shed their seeds and evaluating roadside trees which, because of their increased exposure to sunlight, often bear a heavier crop than trees further in the stand (Dobbs and others 1976).

Filled seed counts.--Final decisions on whether to collect a crop should be based on the amount of sound seeds forming in the cones. In many species, cones will develop without pollination but no seeds will be produced (Allen 1941b; Orr-Ewing 1954; Meagher 1974) so an inspection of the developing seeds is essential. Abundant pollen is required for a good seed set regardless of female strobilus production (Sarvas 1957, 1968; Boyer 1974; Fechner 1979). Heavy male and female flowering usually occur in the same year and this is reflected in a higher yield of sound seeds (Cayford 1964; Roe 1964; Sarvas 1968; Zasada and Viereck 1970; Shearer and Schmidt 1971). Good seeds may be found in relatively small areas even in poor years, but these crops should be carefully inspected before collections are undertaken.

The most common inspection method is to slice the cones longitudinally and count the number of filled seeds so exposed. Minimum filled seed counts to set collection standards (table 5) have been established (Buszewicz and Holmes 1956; Seal and others 1965; Meagher 1974; Dobbs and others 1976) and regression equations based on such data have been developed to predict the amount of good seeds in a cone crop (Buszewicz and Holmes 1956; McLemore 1962; Calvert 1978).

Insect damage to cones and seeds, as well as the presence of disease such as cone rust, should also be evaluated since they can seriously affect seed yields. In light crop years, insects and diseases can destroy the entire crop. The presence of insects is often, but not always, signalled by premature browning of the cones, small holes in the cone scales, accumulations of frass, pitch-like exudations, and a general disfigurement of the cone. If the cone-cutting test reveals that more than half of the visible seeds have been affected, collection is probably not worthwhile.

For Pinus contorta and other species whose cones are serotinous and difficult to slice, it is easier to extract the seeds by dipping the cones

Table 5.--Average number (and range) of filled seeds exposed per half cone, by crop year (Source: British Columbia Ministry of Forests, Silviculture Branch 1985)

Species	Crop year						Minimum count for collectable crop[1]
	1980	1981	1982	1983	1984	1980-1984	
Abies amabilis	9	--	10	12	--	11	8-12
	(5-12)		--	(9-12)		(5-16)	
Abies grandis	--	16	14	--	--	15	12-14
		(11-24)	(12-18)		(11-24)		
Larix occidentalis	3	--	--	--	1	3	6
	(1-5)				--	1-5	
Picea glauca/ Picea engelmannii	7	--	6	4	--	6	7
	(4-10)		(3-8)	(2-7)	--	(2-10)	
Picea sitchensis	--	--	--	5	--	5	5
				(3-6)		(3-6)	
Pinus contorta	(see text)						20 per[2] whole cone
Pinus monticola	11	11	6	--	--	10	90 per whole cone
	(7-15)	(7-13)	(4-8)			(4-15)	
Pseudotsuga menziesii	5	1	4	2	--	5	5
	(1-7)	--	(1-7)	--		(1-7)	
Thuja plicata	7	2	9	--	--	8	4-6 per whole cone
	(2-12)	(1-4)	(6-11)			(1-12)	
Tsuga heterophylla	3	1	5	--	--	4	3
	--	(1-2)	(3-7)			(1-7)	
Tsuga mertensiana	--	--	7	--	--	7	--
			(4-10)			(4-10)	

[1] Figures applicable just prior to collection because insects or disease may decrease counts if there is a significant time lag between examination and collection.

[2] Dobbs and others 1976.

briefly in boiling water then oven-drying them at 65°C for three to four hours. Extracted seeds may then be cut or crushed to reveal a firm white megagametophytic tissue (endosperm) if they are filled. For *Pinus contorta* a minimum of 20 filled seeds per entire cone indicates a collectable crop in British Columbia (Dobbs and others 1976) but experience in Alberta suggests collectability is indicated by a count of only six to eight filled seeds (Hellum and Wang 1985).

CONE COLLECTION

The basic objective of any collection method is to get the cones from the tree tops and into sacks in the most efficient and safe manner without damaging seed quality. All cone collections require advance planning and organization. The larger the collection operation, the more its success depends upon staff training, especially that of the supervisors (Dobbs and others 1976; Calvert 1985). Besides considerations of which species and provenances are to be targeted, cone quotas and the amount of manpower, equipment and storage facilities must be calculated. These have all been reviewed by Dobbs and others (1976).

Since most reforestation seeds will continue to be derived from natural forests, stands of locally important species selected specifically for seed production purposes should be reserved. These reserved stands should be at appropriate elevation intervals in seed zones where substantial reforestation is expected to occur (Pitcher 1966; Dyer 1968; Holmes 1972; Rudolf and others 1974). All collection sites must have good access and an adequate number of well-formed trees of the required species bearing a collectable crop.

The choice of collection method is influenced by several species characteristics, such as cone shape and size, tree crown shape, and the position of the cones on the tree. The collection method must also consider whether the cones occur at the branch ends or along its length, whether they are erect or pendant, and whether old cones are persistent. Cone persistency can be either a problem, as in *Larix* species, or an advantage, as in *Pinus contorta*, since their serotinous nature allows collection of more than one year's crop at a time. Other more minor characteristics, such as the extreme pitchiness in *Pinus monticola* or *Abies* cones, and the tendency for true fir cones to disintegrate at maturity, must also be weighed. The method of collection also depends on the number of crop-bearing trees and their accessibility; scattered crop trees require a different approach from many crop trees along a road or around a

clearing. Age and height of the trees, whether they are in a sub-dominant or lower crown position, and the evenness of the canopy level, if aerial collections are contemplated, must also be considered.

1. Collection Methods

There are four general methods of cone collection: climbing, felling or topping, aerial raking and clipping, and collections from squirrel caches. The advantages and disadvantages of different cone collection methods have been compared by Cornell (1984) (table 6).

Climbing.--Climbing is the oldest traditional method. It uses few items of accessory equipment compared to other methods, and causes minimum damage to the trees, but requires trained personnel skilled in safety precautions and comfortable working at heights. A climber begins picking at the top of a tree and works his way down and around the crown, using a cone hook to pull up branches bearing cones beyond reach. Cones are usually placed in a bag hanging from the worker's safety belt. Cones should not be thrown to the ground, even in sacks. Even mature cones, especially those of Abies species, should be handled gently to avoid bruising or damage to fragile seed coats (Edwards 1982). Collection costs are minimized by climbing only those trees bearing a heavy cone crop (Goddard 1958). Individual trees should be selected on the basis of phenotype and safety criteria. Climbing for cones has been found to be productive when the crop trees are immature and tree heights are less than 15 m, the cones are medium to large, the stand is fairly open, and the crowns full, with well-spaced, sturdy branches. The species suitable for climbing include Pseudotsuga menziesii, Larix occidentalis Nutt., Pinus ponderosa and P. monticola.

Felling and topping.--Tree felling to collect cones has become common in British Columbia. Collections should be coordinated with logging or clearing operations, but trees may be felled specifically for cone harvest if plans are made to recover the merchantable wood later. Felling requires experienced fallers capable of placing the trees so that the tops are readily available for picking. Cones should be removed from only the phenotypically best trees. For safety reasons, all felling must be completed before pickers are allowed to begin work, but picking is then faster than by climbing, and no special tools are required. Collecting from felled trees is best when the crop trees are mature, where there is good access to an adequate number of trees that are not required for future collections, and when capable fallers are available. It can be used for all species except Abies, the cones of which shatter on impact with the ground, and the method is particularly useful for winter collection of Pinus contorta cones, which are more easily detached in cold weather, provided snow does not cover the downed tops.

Table 6.--Some comparisons of cone collection methods (Source: Cornell 1985)

Method	Advantages	Disadvantages
CLIMBING	Best phenotypes selected. Cones picked when ripe. Minimum damage to trees.	High climber hazard. Picking limited to nearby roads. Staff limitation-may not reach all areas at peak ripeness.
FELLING	Faster, less expensive. Less hazard than climbing. Best phenotypes selected.	Some felling hazard. Felled trees need harvesting. Need coordination with logging. Crop trees lost to further collection. Cones need to be picked promptly once trees felled.
AERIAL	Rapid. Limited surface access required. Best phenotypes selected. Cones picked when ripe. Access to all areas. Best method for some species.	Expensive. Requires large operation and extensive planning for efficiency. High pilot hazard.
SQUIRREL CACHES	Low hazard. Requires limited staff training and little special equipment.	Limited control over seed ripening. No phenotype selection. Quotas may not be met.

If trees would not otherwise be felled, or where subsequent utilization of the timber is not feasible, tree topping may be a more suitable method, especially in species where cones are confined to the uppermost crown as in Pinus monticola. Tops may be cut out with a saw by climbers, or brought down with a high-powered rifle using soft-nosed bullets for maximum effect (Dobbs and others 1976), or removed by aerial clipping. Slayton (1969) found climbing and topping Picea glauca trees, followed by stripping the cones by hand, was cheaper than climbing alone. This conclusion was also reached by Calvert (1985) for Picea glauca and P. mariana Mill. (Britt.). Whether trees are felled or tops removed, prompt picking (within 2 or 3 days) may be necessary to forestall cone opening caused by high soil temperatures, or to prevent losses to birds and animals (Stein and others 1974).

Interest in machinery for stripping cones from tops and slash of Picea mariana and Pinus banksiana began in Ontario in the mid-1960s (Haig 1969) and equipment has been developed which can economically strip cones, particularly in Picea mariana, even in light crops (Horton 1984). The increasing demand for tree seeds has spurred other attempts to mechanize cone harvesting. The use of tree shakers has been successful with some species, especially in the southern United States, but this method cannot be employed except where the terrain will allow easy access and operation of the equipment, such as in seed orchards or some seed stands. Tree shakers are most effective on species with cones that are easily detached such as Picea engelmannii, Abies grandis, Pseudotsuga menziesii or Pinus ponderosa (United States Dept. Agriculture 1972), and can remove cones very rapidly; 75% of the total cones on a Pseudotsuga menziesii tree 48 cm d.b.h. and 30 metres tall were removed in 21 seconds (United Nations Food and Agriculture Organization 1968). Shaking may be effectively used on smaller cone crops that would be uneconomic to collect by climbing (Richardson 1967).

Aerial clipping and raking.- Technology is also being developed for aerial collections of cones (Dobbs and others 1977; Apt and others 1979; Hedin 1983) and two systems, clipping and raking, have been approved for use in Canada. Clipping employs a two-man team of a helicopter pilot and a clipper operator who is secured by harness to the aircraft and operates a hydraulic anvil-type pruner or a special electric chain saw. Depending upon the species and crown shape, either cone-laden branches or tops are removed and stored inside the aircraft as it moves from tree to tree. Aerial raking uses a device, suspended below the helicopter, that is lowered over the target tree until the cone bearing top protrudes through the center of the cutter head. When the rake is lifted, the head severs branches which fall into a collection basket. As with clipping, the aircraft moves from tree to tree until a load has been gathered, and flown to a landing for off-loading. For safety reasons, pickers are permitted on the landing only when aerial delivery is complete.

Raking and clipping are suitable for use on mature trees in mixed stands when the cones are in the upper third of narrow, tapered crowns. Clipping is best used when the target trees are dominant or codominant, while raking may also be applied to lower canopy trees when they bear cones. All aerial systems require favorable weather conditions: steady winds of less that 15 kmh, and little or no rain. Both systems can be used for collecting Pseudotsuga menziesii or Picea cones. If used on other species, clipping can become prohibitively costly, but raking is ideal for true firs, and some rakes have been devised for use on Thuja plicata and Thuja heterophylla.

Aerial methods are excellent for harvesting cones from inaccessible stands, from trees in stands protecting streams, or from areas which migratory animals traverse. Because of tariff rates, equipment rentals, fuel costs, time spent training people and organizing and coordinating the collection program, aerial operations are expensive. For cost-effectiveness, both productivity and resulting seed quality must be high, which can only be achieved when there is a heavy cone crop with good seed counts. Nevertheless, the overall costs of helicopter collections have been found to be competitive (Hedin 1983; Cornell 1984), especially for species such as true firs (Wallinger 1985). Since larger quantities of cones can be harvested per day, helicopter collections can be completed in a shorter time frame, which allows them to be started closer to full ripeness of the seeds.

Squirrel caches.- Provided the source stand is of good phenotypic quality, the reforestation value of the seeds obtained from squirrel caches may not suffer unduly since caches are located in the general vicinity of the trees from which the cones are removed. Should the stand contain poor phenotypes, the method should not be used. In light crop years squirrels can seriously deplete a developing seed crop (Larson and Schubert 1970), in some instances leaving very little for the forester to collect (Shearer and Schmidt 1971). Fears that Pseudotsuga menziesii seeds from squirrel-cached cones may be of poor quality because they were cut from the trees before becoming fully mature have been dispelled by Lavender and Engstrom (1956) who observed that some cones were cut prior to full ripeness, but that the squirrels cut cones in quantity, and began caching them, only when the seeds were ripe, and that no significant increases in seed quality occurred with later cutting. Wagg (1964) observed that seed quality in cached cones of Picea glauca was higher than in cones collected from the tree because some of the mature seeds had fallen from partially opened cones on the tree, resulting in an increase in the proportion of under developed seeds in later cone collections. However, since caches are typically found in damp areas in decayed wood or duff, or around old stumps or logs, cones should be checked for the presence of pathogens. Commercial seed merchants frequently collect from caches, yet their product can be of exceptionally high quality.

2. Seed Maturation

One of the crucial considerations in any collection is that the seeds have achieved either full ripeness or a threshold of maturation from which they will continue to develop in the cones before seed extraction begins. A detailed review of seed maturation and its effects on seed quality can be found in Edwards (1980a).

While viable seeds can be obtained long before the cones are ready to open, seed maturity in conifers is usually associated with seed dispersal. Unfortunately not all the cones mature simultaneously, and calendar dates vary with locality and weather patterns. There may be variations in ripening among the cones on any one tree (Ching 1960; Fowells 1949; Maki 1940), among trees in the same stand (Allen 1958b), between different stands in the same year (Fowells 1949) and considerable variation from one collection year to another (Allen 1958a; Fowells 1949). Most conifers release their seeds quickly once maturity has been attained so the period for collecting mature seeds is no more than two weeks in most species. The general conclusion drawn from a multitude of investigations is that the more mature the seeds are when collected, the greater their vigor and potential for establishment of seedlings (Pollock and Roos 1972). Therefore the timing of seed collection has to take into account numerous considerations and if collection is delayed, even by a day or so, the bulk of the crop may be lost.

The cones of some species such as _Pinus contorta_, _P. banksiana_ Lamb. and _Picea mariana_ usually are serotinous, that is the edges of the cone scales are bonded together by resin. Cones of these species may remain intact on the tree for several years after maturation, providing a longer collection "window." In _Pinus albicaulis_ Engelm., intact cones fall from the tree and the seeds are released only after the cones have lain on the ground and have disintegrated over several months (Krugman and Jenkinson 1974).

Among the consequences of collecting cones too early is a high moisture level that favors mold growth. Unless the cones are well ventilated during storage before seed extraction, they may suffer from heating that can cause direct damage to the seeds as well as exacerbate mold activity. The higher moisture content of immature cones requires longer kilning, thereby increasing extraction costs (Roe 1960), and normal kilning temperatures may be lethal to the immature seeds (Matyas 1973). Immature cones may fail to expand fully when kilned and remain closed or semiclosed, thus reducing seed yields (Maki 1940). Immature seeds generally do not retain their viability in storage as well as mature ones (Holmes and Buszewicz 1958), are usually lower in dry weight, may germinate slowly, are more susceptible to disease and produce a higher proportion of abnormal germinants (Edwards 1980a). Olson and Silen (1975) concluded that immature _Pseudotsuga menziesii_ seeds collected around mid-August from a seed orchard required considerably more work to extract them from the cones and produced very light seeds. Nearly all the seeds that were collected early germinated below 10% and germinant mortality was high. They estimated that immature seeds cost 10 times more to produce seedlings than seeds collected just prior to seedfall.

Maturation indices.--Numerous indices of seed maturity have been developed (Edwards 1980a). Physical indices such as cone color, seed color, cone moisture content or specific gravity, seed brittleness, and tissue shrinkage when a cut seed is exposed to the air for several hours, as well as chemical indices including the level of fat, sugar, starch, protein and other constituents in the seeds have been used as indicators of the progress of ripening in many tree species, including broadleaves. Dobbs and others (1976) suggested that embryos should have extended to fill at least 75% of the cavity within the endosperm before cone collections are started. Embryo extension can be easily determined in the field or it can be recorded on x-ray film (Wang 1973). Recent experience has shown that early collections may cause germination problems in the nursery unless the cones are properly stored to allow seed ripening to be completed before the seeds are extracted. For British Columbia species it is now recommended that cone collections be delayed until embryo extension is at least 90% complete, and until the endosperm has changed from a viscous, milky consistency to a white, firm state resembling the edible portion of a coconut (Rooke 1985). Embryo maturity is related to summer heat and in severe climates the best seeds may be found on southern aspects or on the south-facing side of the crowns. The utility of heat sums to predict the time of cone collection in _Pinus ponderosa_ has been discussed by Tanaka and Cameron (1979). Degree-day summations for judging seed maturity have been used in Scandinavia but are not widely used in North America (Edwards 1980a).

Other characteristics that should also be checked when judging cone ripeness have been compiled by Wallinger (1983) for west coast conifers. An illustrated guideline for estimating when to collect seeds of some eastern species including _Picea glauca_, _P. mariana_, _P. pungens_ and _Pinus banksiana_ has been recently produced also (Ontario Ministry of Natural Resources 1984).

Artificial ripening.--Prematurely collected cones, containing immature seeds, require special care prior to seed extraction. The seeds of several conifers, including _Pseudotsuga menziesii_ (Silen 1958), _Picea glauca_ (Zasada 1973; Edwards 1980a; Winston and Haddon 1981,) _Larix occidentalis_ (Shearer 1977), as well as several _Abies_ species (Rediske and Nicholson 1965; Pfister 1966; Oliver 1974) and the major southern pines (Wakeley 1954) will continue to ripen in the cones after harvest if they are properly stored. The conditions for successful artificial ripening remain ill-defined, but where success has been obtained in the Pacific Northwest, air temperatures between 5° and 10°C, relative humidities of 65%-75%, and good air circulation around the cones have all been implicated (Edwards 1980a). In other words the cones should be kept cool and well ventilated but

should not dry out too quickly. Cones collected 4 to 6 weeks prior to natural seedfall have produced high quality seeds when artificially ripened for 1 to 2 months. The earlier cones are collected, however, the more sensitive they are to storage conditions or, conversely, the more easily seed quality can be damaged (Zasada 1973). The provision of adequate artificial ripening facilities in the field raises additional problems, and expenses, but when large collections are contemplated, an early start might make the difference between sufficient cones being collected and quota shortfall.

3. Cone Storage in the Field

Even when cones with fully mature seeds have been harvested, seed quality can be impaired at almost every subsequent step. Cones may be transported to the processing plant immediately after harvest, but more likely they will be assembled at a shipping depot in the field. This provides an opportunity to clean them of excessive debris which, if it is not removed, may complicate later seed cleaning.

If the cones were wet when sacked, they can be spread out at the shipping depot and air-dried, then resacked. Proper interim storage at the shipping depot allows the cones to "cure," that is, lose some moisture as they continue to ripen. For this, individual cone sacks should be exposed to free movement of air. Additional heating, by direct sunlight for example, and rewetting must be avoided. Protection from rodent depredations may also be required. Portable racks (Stein and others 1974) or trestles (Dobbs and others 1976) set up in well-shaded locations, or open sheds, some of which are portable (Wallinger 1982), can readily provide the right conditions. Cones of _Abies_ spp. are particularly susceptible to heat buildup and molding, especially if moist when sacked. They should be placed in screen-bottomed trays at the interim storage shed, or as soon as they reach the processing plant. Fans may be required to provide adequate ventilation. Since the cones of most conifers expand as they lose moisture, sacks should not be overfilled in the field, otherwise the scales may acquire a set that severely impairs seed extraction (Stein and others 1974; Dobbs and others 1976).

4. Cone Transportation

Seeds can be injured during transportation if the cones are freshly picked, and more so if they were picked prematurely. Allowing the cones to air dry at the interim storage depot, for 4 to 6 weeks for some species, makes transportation conditions less critical. Even so, cones remain perishable. Even after sufficient drying, travel times to the processing plant must be kept to a minimum, and the cones kept cool and well ventilated. The use of refrigerated trucks for cone shipment is now advocated in British Columbia (Johnson 1984) and for moving tops of trees in Ontario (Horton 1984). Truck drivers should be informed of the perishable nature of their loads, the need for proper care, and prompt delivery of their cargo. Field collection supervisors should advise the processing plant in advance of shipments so that the necessary staff will be available for prompt unloading of the cones (Dobbs and others 1976).

5. Cone Storage at the Processing Plant

Some of the cones cannot be processed immediately because of equipment limitations, but in many cases cones are stored for a further period to ensure additional drying. Specially designed sheds are normally used for this purpose (Stein and others 1974). For most species there is a period of safe storage (table 7) and seed extraction schedules need to be prepared accordingly. Cones of several British Columbia conifers have been stored for up to 6 months without loss of seed quality (Leadem 1982), but shorter periods are preferred since there is a danger of seed mortality or germination in the cones. For example, seeds in cones of _Tsuga heterophylla_ and _Thuja plicata_ may germinate before they can be extracted, so these species should be scheduled for early processing. Cones of _Abies_ spp., on the other hand, are often stored for 2 months or longer, until they have completely disintegrated and do not have to be kilned. By then the seeds will be fully ripened.

Table 7.--Safe storage periods in sacks for cones of western conifers (Source: British Columbia Ministry of Forests 1985)

Species	Storage period (months)
Abies amabilis _Abies grandis_ _Abies lasiocarpa_	2-4 (in trays)
Larix occidentalis	3-5
Picea engelmannii _Picea glauca_ _Picea sitchensis_	3-5
Pinus contorta	4+
Pinus flexilis _Pinus monticola_ _Pinus ponderosa_	3-5
Pseudotsuga menziesii	3-5
Thuja plicata	1
Tsuga heterophylla _Tsuga mertensiana_	1

CONE AND SEED PROCESSING

Technically, processing includes all treatments applied from the time the cones arrive at the processing plant until the seeds are prepared for sowing in the nursery. For the purposes of this review, however, only those steps leading up to cold storage will be discussed.

Upon delivery to the plant, cone sacks are identified by seedlot and stored until scheduled for processing which begins with cone drying or kilning, continues with tumbling and dewinging, and ends with cleaning and sorting. Depending upon the species and the methods employed, up to five stages may be involved in processing extracted seeds (fig. 1).

1. Kiln Drying

The objective of kilning is to open the cones quickly without damaging seed viability, so the heat must be carefully controlled (Rietz 1941; Carmichael 1958). Usually, the scales of most cones have already begun to open, but additional drying is needed to fully flex the cones into an open position to enable maximum seed recovery. Cones should be exposed to an air flow of gradually decreasing moisture content and rising temperature up to a maximum between 40° and 50°C for most species near the end of the drying period. Rapid kilning of cones still high in moisture content removes moisture from the outer layers of the scales, which partially flex and then set in a semi-open position preventing seed release. This condition is known as "case-hardening" (Edwards 1981). The risk of case-hardening is reduced if the cones have been well cured, i.e., air-dried during storage. In addition, wet seeds exposed to high kiln temperatures at the beginning of the process would likely be scalded. If the cones were too tightly packed in the sacks, full opening of the scales may not occur even if drying is slow and prolonged. In some processing plants cones may be moved from the storage sheds to a ventilated loft above the kiln where escaping heat aids the drying process. This reduces kilning time and heating costs, and minimizes the chance of seed damage (Allen 1957). Once again the importance of proper cone curing, or conditioning, between the time of harvest and the start of processing is emphasized; properly handled cones require less heat so less damage to the seeds is likely, resulting in a high quality product at lower cost.

Various kiln schedules (Wang 1973; Schopmeyer 1974) have been designed to dry and open cones in the shortest possible time without damaging seed viability or causing case-hardening. Most cones in British Columbia are dried in less than 16 hours (table 8), but immature cones and those attacked by insects usually do not completely open even after extended kilning. When cone scales have fully flexed the seeds fall out easily during tumbling and should be removed from the heat as soon as possible thereafter.

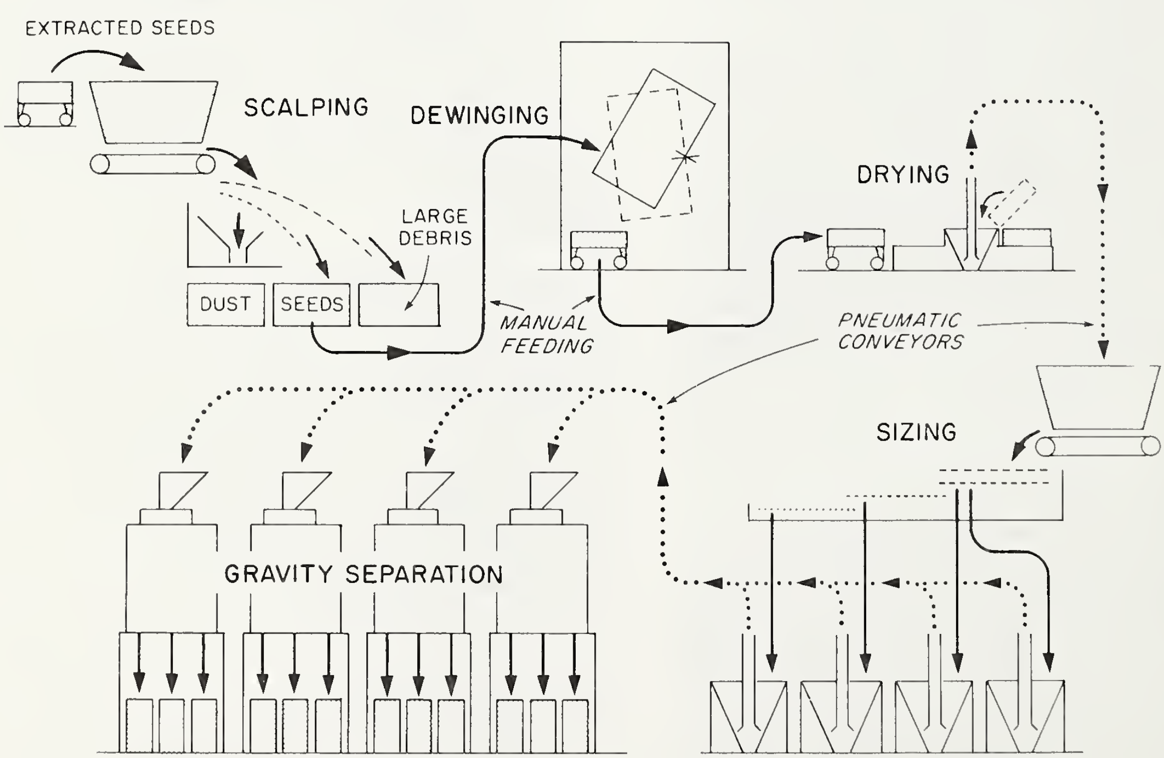

Figure 1.—The five main stages of seed processing: scalping, dewinging, drying, sizing and gravity separation. Some stages may be omitted depending upon the species and methodology. (Diagram based on the Hilleshög, Sweden, processing system which moves seeds by manual means between the early stages and pneumatic means between later stages.)

The outer scale edges of serotinous cones of Pinus contorta var. latifolia are bonded together by a resin-like material, the exact nature of which is not known (Hellum and Wang 1985), although it melts at temperatures above 45°C (Cameron 1953). A widely used method for breaking the bond has been to dip the cones for about one minute in water at 80°-90°C, after which they are kilned for several hours at 60°C (table 8). A newer method of breaking the resin bond uses a scorching device (MacAuley 1975) that briefly exposes cones to high temperatures. Using this process, Hellum and Wang (1985) have recommended that Pinus contorta cones be "cracked open" by using a flash of heat (210°-230°C for 1.5 minutes), after which they are lightly misted with water, then kilned. A cone moisture content of 15-20% at the start of kilning is optimal for good seed yields regardless of the condition of the cones up to that time (Hellum 1981; Hellum and Barker 1980; Hellum and Wang 1985). Most seeds are released within about 6 hours of kilning at 60°C; longer schedules increase the amount of empty seeds (Hellum 1981).

Kilns are essentially over-sized ovens. A basic type consists of a large chamber equipped with heaters, humidifiers and fans. Cones are spread evenly on shallow trays that are stacked on movable carts or dollies. The kiln is loaded with a batch of cones which are processed for the prescribed time, removed when cool and a fresh batch loaded. Such kilns can process large volumes of cones at one time, but all cones in a batch are subject to the same kilning conditions. Another disadvantage is that seeds that fall out of the cones must remain in the kiln exposed to the high temperature until the end of the batch schedule.

In some plants, kilning and tumbling are performed simultaneously in a rotating drum kiln that contains, within the heating chamber, a tumbler that shakes the seeds loose from the cones (Lowman 1975). This type permits loose seeds to be removed from the heat at the earliest possible time, but like the chamber kiln, this is also a batch-type unit. Other kilns provide continuous, on-line drying by employing a tunnel along which the temperature progressively rises. Carts laden with cones on trays move slowly from the cooler entrance of the tunnel to its hotter exit. A variation of this type consists of a conveyor belt on which thinly spread cones move slowly through a long heater box (Gradi 1973). Various types of kilns were reviewed by Sziklai (1981). McConnell (1973) described a small portable kiln designed to dry small lots of pine cones featuring economy, safety, portability and versatility.

Any artificial heating involves a fire hazard and the dust, resin and dry cone scales are particularly inflammable (Morandini 1962; Stein and others 1974). Stringent fire precautions, including a ban on smoking, should be enforced, and fireproof construction materials should be used throughout. Arrangements for removal, by vacuum or other means, of inflammable dust and debris are essential, and dust masks should be worn by operator to reduce the health hazard.

2. Cone Tumbling

Immediately after kilning, cones are tumbled in horizontally-rotating, screened drums or cylinders to shake the seeds free. In rotating drum kilns the tumbler is programmed to revolve at intervals during the drying process so that the seeds can be removed from the heating chamber at the earliest possible time . If tumbling is delayed too long after kilning the open cones may reclose if they are exposed to moist air (Morandini 1962). During tumbling, seeds and small-sized debris fall through the drum screens into a collector or onto a conveyor belt. While some tumblers are enclosed at both ends and must be stopped for loading and unloading (Morandini 1962), more modern designs employ an open-ended, inclined cylinder. Cones are fed in at the higher end and the inclination of the drum can be altered to control the time the cones are tumbled (Turnbull 1975) so the operation can be continuous. Laboratory-sized tumblers for use in research have been described by Winjum and Ellis (1960) and Harris (1970).

Tumbling should be as brief and as gentle as possible. Prolonging the action tends to shake a higher proportion of poorly developed seeds loose and increases the amount of debris caused by cone breakage (Morandini 1962). Speed of rotation and time of tumbling must be adjusted to the cone and seed characteristics of the species. In Larix decidua Mill. and Picea abies (L.) Karst, for example, long periods of tumbling may be necessary since the seeds are frequently tightly held (Aldhous 1972).

With some species, remoistening the cones after one tumbling then redrying and additional tumbling has improved seed yields (Eliason and Heit 1940). After a first tumbling, Pinus sylvestris cones were soaked in water at 30°C for some 30 minutes, until they softened and began to reclose, and were then air-dried so that the scales opened again. The yield of seeds from the second tumbling averaged 36% of that of the first, thereby justifying the extra cost of the process (Van Haverbeke 1976). A large proportion of the seeds removed in the second tumbling are empty or poorly developed and difficult to remove in seed sorting. Seeds processed this way should be kept separate and used quickly since they may not store well (Baldwin 1942).

Some processors use screen-bottomed, tray shakers about 15-20 cm deep, the seeds falling through into a catchment bin beneath. This method is ideal for collections from seed orchards or other small lots.

3. Scalping

Following their removal from the cones, seeds are processed to remove unwanted debris, to remove the membranous wings which greatly increase their bulk and make nursery handling very difficult, and to separate empty or otherwise non-viable seeds.

Table 8.--Cone-processing schedules used in British Columbia (Source: British Columbia Ministry of Forests 1985)

Species	Time in 80°-90°C water	Air-drying period	Kiln-drying period Time	Kiln-drying period Temperature
	seconds	days	hours	°C
Abies amabilis		60-180	6-14	29-30
Abies grandis		60-180	6-14	29-30
Abies lasiocarpa		60-180	6-14	29-30
Larix laricina			8	49
Larix occidentalis			7-9	43
Picea engelmannii		20-50	6-24	38-49
Picea glauca		20-50	6-24	38-49
Picea mariana			5-11	54
Picea sitchensis		20-50	6-24	38-49
Pinus albicaulis		15-30		
Pinus contorta				
var. contorta		2-20	96	49
var. latifolia	30-60	2-30	6-8	60
Pinus flexilis		15-30	0	
Pinus monticola			14	43
Pinus ponderosa			3	49
Pseudotsuga menziesii				
Coast (var. menziesii)		8-21	2-10	32-43
Interior (var. glauca)		14-60	16-48	38-43
Thuja plicata			24-36	33
Tsuga heterophylla			16-48	30-43
Tsuga mertensiana			16-48	30-43

Immediately after tumbling the seeds still have their wings attached, and to separate them from the debris they are passed over a scalper, which consists of two or more vibrating, inclined screens, one above the other, of progressively finer mesh from the upper to the lower screen (Lowman 1975) (fig. 2). Seeds are usually retained on the intermediate screen. "Tappers" are often used to keep the particles in motion, while moving brushes under the screens reduce seed lodging in the perforations. Dust and chaff are removed by an exhaust hood.

4. Dewinging

Seedwing removal serves primarily to facilitate subsequent cleaning and to reduce the volume of material placed in cold storage and to improve the field sowing characteristics of the seedlot. In older processing plants, seed dewinging was the operational step during which seed damage through crushing, cracking or abrasion was most likely to occur (Eliason and Heit, 1940; Allen 1957; Kamra 1967; Wang 1973), but newer equipment has minimized or eliminated the danger. Excessive dewinging must be avoided since germination can be seriously damaged, the seeds seem to be more easily contaminated by mold and the resulting seedlings are weak (Baldwin 1942).

Wings are attached to the seeds by different means in different species; for example, in Pseudotsuga menziesii seeds the wing is an integral part of the seedcoat and must be mechanically broken off, while in pines and spruces the wings weakly encase the seeds and can be removed with much less abrasive action. Seeds of Abies spp. are particularly susceptible to damage to their fragile seedcoats (Edwards 1982), the reduction in viability being related to rupturing of the several resin vesicles (Gunia and Simak 1970; Kitzmiller and others 1973, 1975). Allen (1957) observed that seeds of Abies lasiocarpa that were passed three times through a brush dewinger lost 50% of their original viability. For Abies concolor (Gord. and Gledl.) Lindl. and A. magnifica A. Murr.

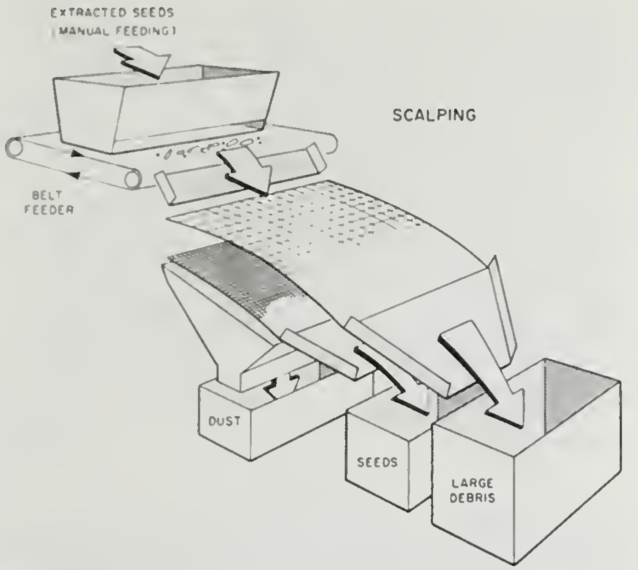

Figure 2.--Seed scalping to remove particles larger and smaller than the seeds. The interchangeable screens are vibrated electromagnetically. (Diagram based on the the Hilleshög Co., Sweden, equipment.)

seeds, Kitzmiller and others (1975) recommended the use of a scalper treatment followed by pneumatic separation as the least damaging method.

Wings are small or impractical to remove from the seeds of several genera including _Thuja_, _Cupressus_, _Chamaecyparis_ and _Libocedrus_. Seeds of _Juniperus_ are wingless, and since they are produced in fleshy indehiscent strobili, commonly called "berries," quite different processing procedures must be adopted. These methods have been reviewed by Stein and others (1974) and Johnsen and Alexander (1974).

Dewinging methods for other conifers are generally categorized as either dry or wet.

Dry dewinging.--Dry dewinging involves rubbing the wings off mechanically, and the simplest and safest method is to gently hand rub the seeds in a sack, but this is practical for small quantities only. One of the simplest mechanical devices is a wire screen or perforated plate, the holes of which are large enough to allow the seeds to pass through but not the wings. A soft brush works the seeds against the screen while a draft of air draws off the wing fragments. Many types of mechanized dewingers, mostly rotating devices, have been developed (Lowman 1975). These may have brushes, rotating knobs or paddles which force the seeds through narrow outlets, breaking off the wings (Morandini 1962). Distances between the knobs, paddles, brushes and cylinder wall must be adjusted so that there is neither too much pressure that could crack or break the seedcoats nor too much friction that could cause heat damage. Lowman and Casavan (1978) designed a small-lot dewinger consisting of a rubber-lined, inclined cylinder with a rotating central shaft to which are attached pure gum flaps. Another type of dewinger employs a vertical cylinder inside of which is an auger that lifts and rubs the seeds against one another. Some operators add a small amount of coarse debris to enhance the rubbing action that breaks off the wings. In British Columbia this type of dewinging has proven very effective on seeds of _Pseudotsuga menziesii_ and _Larix occidentalis_.

Wet dewinging.--The wings of _Pinus_ spp. and _Picea_ spp. are attached by means of a two-pronged depression that grips the seed (pine) or by means of a spoon-shaped hollow partially enclosing the seed (spruce). Since the wings are more hygroscopic than seeds, they expand when wet and loosen their grip on the seeds from which they can be separated cleanly with minimal agitation in a short time (Wang 1973). This is the basis of wet dewinging, a method formerly believed to impair seed quality and storability. But only a small amount of moisture is required, and since the separation process is quite rapid, the moisture content of the seeds does not increase markedly. A jet of air can be employed to blow the wings out of the mixer and simultaneously begin to redry the seeds (fig. 3).

Several types of dewingers are in use. Many are cement mixers with modified paddles, the slow rotation of which rubs the wings loose while they are lightly sprayed with water. Prolonged wetting should be avoided and it is important that the seeds be redried promptly to avoid any diminution of viability. Seeds are usually dried in a thin layer spread on fine-screened trays through which warm (<30°C) air is blown (fig. 4). It can also be carried out in a cabinet-type dryer (Lowman 1975), or a chamber-type cone kiln if it is not in use. New forced-air seed drying equipment has been developed recently in Great Britain (Waddell 1984), while a compact, multiple compartment tumbler drier was described by Leadem and Edwards (1984).

5. Seed Cleaning and Sorting

In some processing plants, seed cleaning is inseparable from sorting the better grades of seeds from incompletely developed or empty ones. After dewinging there may still be some detached wings among the seeds and further separation is required. This increases the precision with which the seeds can be mechanically sown in the nursery.

Three cleaning and sorting systems are commonly used; screens, air columns and gravity (vibrating) tables.

Screens.- One of the simplest cleaning systems is based on particle size, which is the principle of the scalper described earlier. When this is combined with an air current so that dust, chaff and light, empty seeds are blown away from the oscillating screens, the machine becomes a fanning mill. Air flow, mesh size, screen inclination,

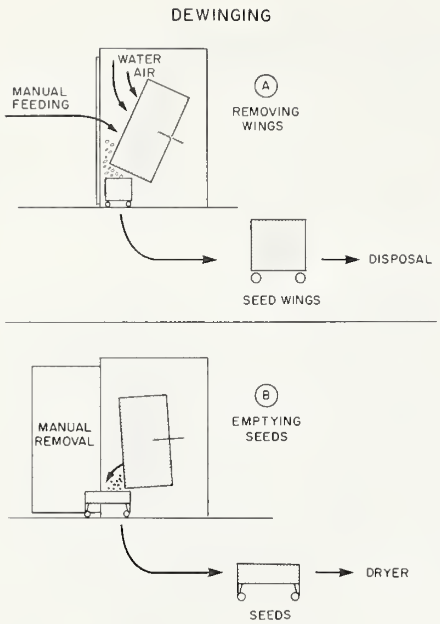

Figure 3.--Wet dewinging using a rotating barrel similar to a cement mixer. Water is added to swell the hygroscopic wings which release the seeds. An air jet blows out the loose wings and begins to redry the seeds. (Diagram based on the Hilleshög Co., Sweden, equipment.)

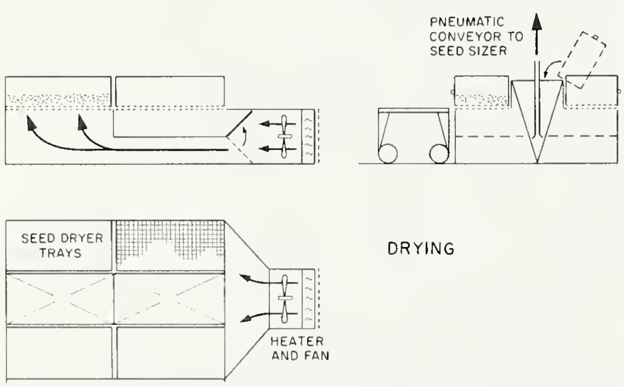

Figure 4.--Seed drying using a tray system through which warm air is forced. The drying bench is designed for easy handling of the trays. (Diagram based on the Hilleshög Co., Sweden, equipment.)

distance travelled and rate of oscillation are all usually adjustable and in some instances the fanning mill may produce the final product. For some species, or seedlots, the fanning mill is only an intermediate step and more precise cleaning has to be obtained by other means.

Air columns.--These employ a vertical air current. Separation depends on the relative rate of fall of seeds with the same surface area but different weight, or those of uniform weight but different surface area. Filled seeds sink while empty seeds are carried away by the rising air current, the velocity of which can be adjusted to suit the species. For this method to work, it is important that the seeds have been completely dewinged, since any wing remnants will increase the proportion of seeds blown away. The South Dakota blower (Erickson 1944) is one of several devices (United States Department of Agriculture 1952; Silen 1964; Hergert and others 1966; Woolard and Silen 1973; Lowman 1975; Edwards 1979) based on this principle. The efficiency of air separation is improved if the seedlot has been previously sorted into uniform size classes (fig. 5). After separation, the filled seeds from all size classes are recombined (fig. 6).

Gravity tables.--An apparatus originally developed by the mineral industry to separate ore from clay and to grade ore has been adapted by the seed industry (Lowman 1975). The specific gravity table comprises an oscillating, inclined, perforated deck, the adjustable slant and vibratory motion of which causes the seeds to move while air is forced up through the perforations, separating the seeds into layers, or strata, of different densities. Heavier particles, such as stones or dried pitch fragments "track" uphill, while the airstream "floats" lighter materials down slope. Three basic rules govern this type of sorting: a) seeds of the same size but different densities can be separated, b) seeds of different sizes but the same densities can be separated, but c) seeds of different sizes and different densities cannot be readily separated (Vaughan and others 1968; Thomas 1978). Movable dividers on the discharge edge of the table allow the seeds to be divided into a number of different density fractions. The process is rapid and efficient (Switzer 1959) and is continuous as long as the feed hopper contains seeds.

There is little evidence that gravity sorting or air separation causes seed damage, although either process might exacerbate injuries caused by other treatments. Pneumatic separation inflicted some resin vesicle damage in *Abies concolor* and *A. magnifica* seeds but it eliminated impurities and empty seeds, and was less damaging than other cleaning methods (Kitzmiller and others 1975).

Other cleaning and sorting methods for tree seeds have been described, including an inclined belt (Hergert 1971; Lowman 1975), magnetic, electrostatic, and conductivity devices (Bonner 1978; Karrfalt and Helmuth 1984), and flotation in various liquids (Baldwin 1932; McLemore 1965; Lebrun 1967; Barnett and McLemore 1970; Simak 1973; Barnett 1976). Barnett (1971) and Edwards (1980b) reported reductions in viability when organic solvents were used as seed separating agents. Attempts to use water as the separating medium were only partially successful (Edwards 1980b) until Simak (1981; 1983; 1984) described the "IDS" method. In the IDS process, seeds are soaked in water, then incubated for several days, then dried. Under the appropriate drying regime,

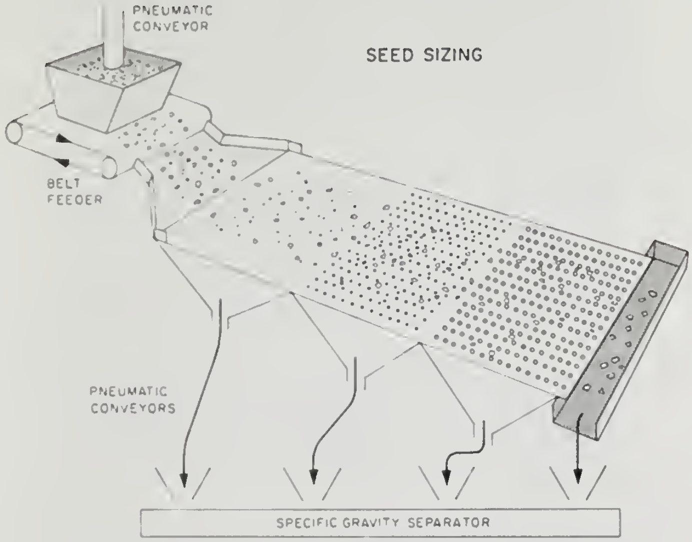

Figure 5.--Seed sizing, shown diagrammatically using a single, vibrating screen with progressively larger perforations. Several screens stacked vertically are typical. Each seed-size class is then sorted separately. (Diagram based on the Hilleshög Co., Sweden, equipment.)

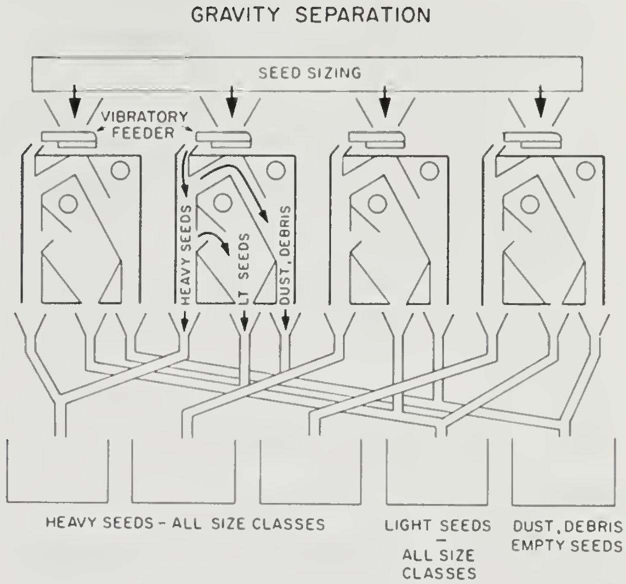

Figure 6.--Seed sorting using aspirator separators. Seeds from each size class are fed into devices from which air is drawn by vacuum. Air speed through each separator is controllable so that heavy (filled) seeds fall against the air stream while lighter seeds are drawn into a separate chamber. Dust and debris are drawn into a third chamber. Seeds from all size and weight classes are recombined. (Diagram based on the Hilleshög Co., Sweden, equipment.)

viable seeds retain all or most of their moisture, while dead seeds dry out. This difference in moisture content causes live seeds to sink, and dead seeds to float, when the mixture is again placed in water. Using this method, Pinus contorta seeds were improved from 67% to 96% germination capacity, retaining 72% of the original seed bulk (Simak 1984), and from 85.0% to 92.5%, retaining 91.5% of the original bulk, and from 77% to 96.5%, retaining 78% of the original bulk (Edwards and others 1985). IDS processed seeds can be stored for at least two years (Edwards, unpublished). The method is being tested on other British Columbia conifers with a view to developing a procedure for use on a large scale (Edwards, unpublished).

The efficiency of all seed cleaning and sorting methods can be checked by periodically cracking or cutting samples of the processed seeds. X-ray techniques (Belcher 1973; Eden 1965; Edwards 1982) are faster and less destructive. Partially filled seeds should be removed since these are often a cause of fungal contamination of the seedlot, especially in pine seeds (Rowan and DeBarr 1974). After cleaning, seeds must be thoroughly mixed to ensure a homogeneous seedlot, and moisture levels must be adjusted to ensure that they meet required standards before they are placed in low temperature storage.

As noted earlier, processing normally continues with seed preservation in cold storage until needed for sowing in the nursery, with germination testing and, in some seed plants, with preparation of the seeds for sowing. However, these topics are beyond the scope of this review. Interested readers will find that tree seed storage has been well covered by Holmes and Buszewicz (1958), Stein and others (1974) and Wang (1974), and it was the subject of a recent international symposium (Wang and Pitel 1982). Tree seed testing was thoroughly described by Bonner (1974) and the special needs for the true firs were detailed by Edwards (1982). Presowing treatments have been reviewed by Bonner and others (1974).

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CAN WE ATTAIN BRITISH COLUMBIA SEED PRODUCTION GOALS FOR INTERIOR SPRUCE?

Paul J. Birzins

ABSTRACT: The British Columbia seed production target is 4,000 viable seeds per interior spruce ramet per year by age 15 (15 years from grafting). In 1983, 10-year-old ramets produced an average of 65.4 cones and 27.6 filled seeds per cone, resulting in a mean filled seed production per ramet of 1,805. One year later production was substantially lower at 46.46 filled seeds per ramet when the average number of cones per ramet was 10.1 and filled seeds per cone was 4.6. Based on this information, orchard location, and associated cone induction trials, the chances of attaining the seed production target are discussed.

INTRODUCTION

Estimated cone and seed yields from grafted ramets and future seedling requirements are used to determine the size of seed orchards in the cooperative British Columbia Tree Improvement Program. Failure to meet seed production targets will limit the positive impact of our reforestation and tree improvement programs on the forest economy. Therefore, the accuracy of seed production estimates must be continually updated to determine the level of seed production from orchards in relationship to seedling demand. If these figures are not updated, seed collections from natural stands and from orchards may become out of balance with seedling demand, resulting in considerable financial loss. For example, if seed production from the orchards falls below target levels, collections from natural stands will be required to reach the seed production goal. If orchard production is not determined in time to collect seed from the natural stands or there is not a good inventory of seed from the designated seed zone, the seed shortfall could result in a slowdown in reforestation. This would result in a loss of desirable species on productive growing sites, which would eventually lead to a decrease in the annual allowable cut for the area.

Projected annual seedling requirements for British Columbia (BC) indicate that interior spruces (*Picea glauca*, *P. engelmannii*, and their hybrids) will continue to be the major reforestation species. Recent data for the BC interior show that anticipated annual demand by the year 2000 for interior spruce will be 86.1 million seedlings (Albricht 1985). This high interior spruce seedling demand has resulted in the allocation of a major part of tree improvement funding into grafted clonal seed orchards and associated breeding activities for the species. To date about 30 ha (96 acres) of spruce seed orchards have been established.

Our spruce seed production estimates are based on extrapolation from extremely limited data. Expectations are that by age 15 (15 years from grafting) each orchard ramet should be producing an average of 100 cones with 40 filled seeds per cone for a total of 4,000 viable seeds per ramet. Relatively recent literature indicates that this estimate may be high. Ten- to 19-year-old white spruce ramets had considerably lower production of viable seeds (2,262 per ramet) but higher cone yields of 174 cones per ramet (McPherson and others 1982). The relatively small number of filled seeds per cone (13) has also been reported for black spruce (*P. mariana*) (McPherson and others 1982; Verheggen and Farmer 1983).

Our first clonal orchard was established at Skimikin, BC (lat. $50^{\circ}47'$, long. $119^{\circ}14'$) in 1979 and therefore is too young to provide meaningful seed production information. Fortunately, in 1976 G. Kiss, BC Ministry of Forests spruce breeder, established a breeding arboretum at Vernon (lat. $50^{\circ}15'$, long. $119^{\circ}14'$) which is located in the hot, dry Okanagan Valley. The spruce program was originally located considerably farther north (3° of latitude); however, greater strobili production was anticipated in the Okanagan Valley, and this has been confirmed (Kiss, 1978). Based on this fact, the majority of spruce seed orchards are located in the Okanagan Valley.

WHAT ARE CURRENT SEED PRODUCTION YIELDS?

To update spruce seed yield estimates, cone and seed data were collected from clones in the oldest section of the East Kootenay breeding arboretum in 1983 and 1984.

Materials and Methods

The ramets in the East Kootenay breeding arboretum located at Vernon, BC were planted at a 5.5- by 5.5-m (18- by 18-ft) spacing on an orthic black chernozem soil (Grandview Series) from 1976 through 1979. The 1.5 ha (3.7 acre) arboretum consists of 127 clones planted in clonal row plots (4 ramets per clone). Scions were collected from ortets

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located between latitudes $49^{\circ}01'$ and $50^{\circ}52'$, longitudes $114^{\circ}18'$ and $116^{\circ}36'$, elevations between 854 and 2 012 m (2,800 - 6,597 ft) and grafted onto 2-year-old rootstock using the side veneer technique. The 235 ramets selected for the study were grafted from 1972 through 1974, planted in 1976, and were about 2 m (6.6 ft) tall in 1983.

Bulk collections of 10 cones per ramet were made in the fall of 1983 from those ramets that had produced a sufficient number of cones. Cones were oven dried for 12 hours at 50° to 70°C (122° to 158°F). Seed was extracted by hand, dewinged, and the filled seed fraction was determined using a single-tube South Dakota blower. A sample of filled seeds in this fraction was counted and weighed. This weight was then divided into the total seed weight to determine the total number of filled seeds. Since this figure represented 10 cones, the total weight was divided by 10 to determine the number of filled seeds per cone. The study was repeated in 1984.

Results and Discussion

In 1983 the average number of cones per ramet was 65.4 (range 0-500) and the average number of filled seeds per cone was 27.6 (range 0-89). This resulted in a mean filled seed production per ramet of 1,805, which contrasted with the significantly lower production figure of 46.46 filled seeds per ramet that occurred in 1984 when the average number of cones per ramet was 10.1 (range 0-250) and the average number of filled seeds per cone was 4.6 (range 0-20). This cone and seed production information is summarized in table 1. According to local observations, in 1983 there was good male strobili production and the cone crop was the largest since the establishment of the arboretum. The 1984 cone and pollen crop was classified as very light, using the classification criteria outlined by Dobbs and others (1976). About 97 percent of the total seed production during these 2 years occurred in 1983. Cone crops in spruce stands were of similar proportion. In 1984 at a 15-year-old East Kootenay spruce clone bank near Prince George (about 3° of latitude north of Vernon) there were absolutely no cones and in 1983 there was a medium crop. This clone bank consists of ramets from the same clones as the ramets used in this study. This supports the inverse relationship between cone production and latitude.

As illustrated in figures 1 and 2 there was an extremely unequal clonal contribution to seed

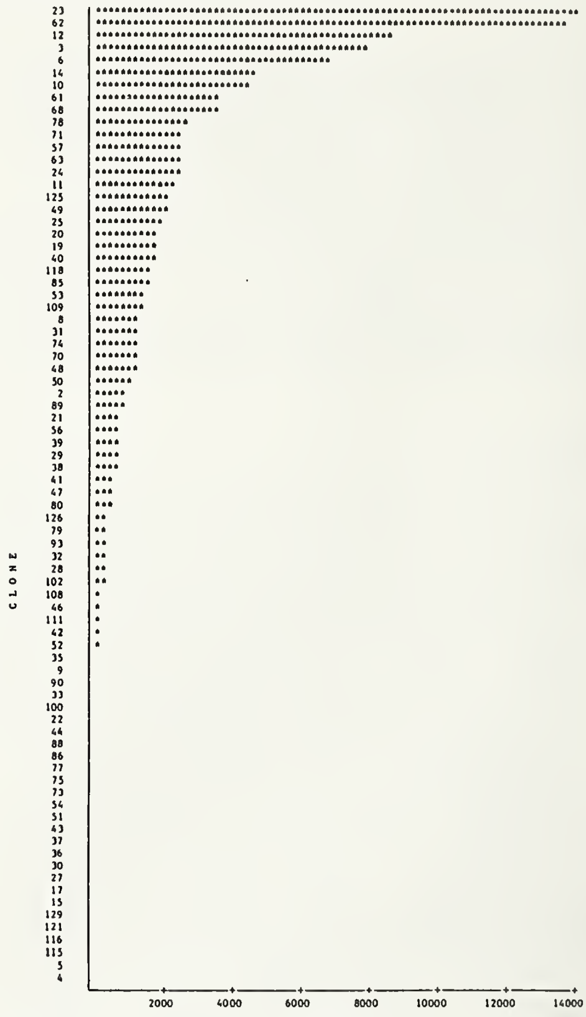

Figure 1.--Mean seed contribution per ramet by clone in 1983.

Table 1.--Summary of cone and seed production from 10-year-old and 11-year-old interior spruce ramets located at Vernon, BC

Variable	10-year-old ramets (1983 data)	11-year-old ramets (1984 data)
No. of clones	79	85
No. of ramets	235	235
Average no. of cones	65.4 (range 0-500)	10.1 (range 0-250)
Average no. of filled seed per cone	27.6 (range 0-89)	4.6 (range 0-20)
Mean filled seed production per ramet	1805	46.46

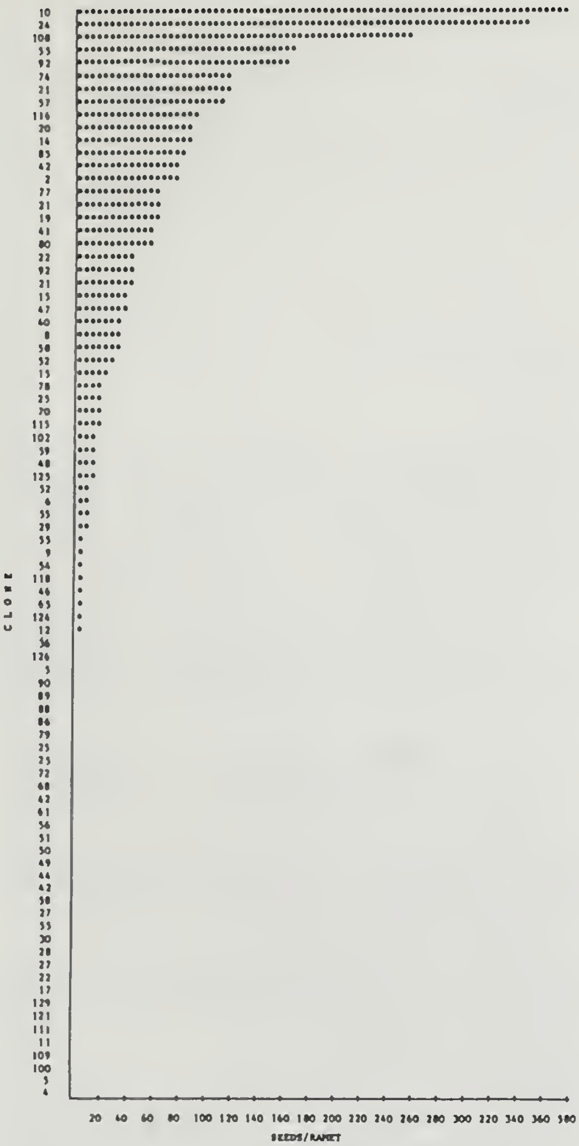

Figure 2.--Mean seed contribution per ramet by clone in 1984.

production in both the marginal and bumper crop years at the arboretum. The discrepancy between clonal number (79 clones in 1983 compared to 85 clones in 1984) is attributed to seed extraction difficulties during 1983. The ANOVA for both years indicates significant differences in cone production per clone (0.01 level). In an unmanaged seed orchard the pollen mix and cone production can be very poor, as shown in the 1984 data.

Ideally, we want equal amounts of pollen and cone production per clone to maximize the genetic quality of the seed. An unequal strobili distribution per clone implies increased selfing levels and therefore decreased genetic quality. This problem could also be aggravated by nonsynchronous flowering in the orchard or lack of a pollen crop of significant size. Utilization of supplemental mass pollination techniques rapidly becomes an essential orchard management tool for maximizing the quantity and quality of seed.

CONE PRODUCTION FROM TRANSPLANTED RAMETS

Our seed orchard staff has consistently observed substantial increases in spruce cone production in the year following seed orchard establishment. For instance, no cones were observed on 111 3-year-old ramets when planted at a nursery. One year after transplanting the ramets into a seed orchard, each ramet had an average of 88 cones. A similar number of ramets from the same clones that had been established in the orchard 2 years earlier had an average of only two cones per ramet.

Average heights of the two groups of ramets were quite similar (transplanted trees 134 cm [4.4 ft], orchard trees 140 cm [4.6 ft]). Obviously, transplanting accounted for the additional cone production. Eighty-one of the transplanted trees were over 100 cm (39.4 ft) tall and had an average of 14.9 cones per tree. The data from this study are summarized in table 2. With increasing size of transplanted ramets there was a pronounced increase in cone production in the year following transplanting.

DISCUSSION AND CONCLUSIONS

If the goal of 4,000 filled seeds per ramet by age 15 is to be reached, a 67 percent increase in seed production will be required in 4.5 years. The breeding arboretum is not managed as a production seed orchard; however, the cone production data suggest that unmanaged seed orchards could yield well below their biological potential. Further decreases in seed production could occur if cone and seed insects "discover" our seed orchard sites. Presently the seed orchards are isolated from natural spruce stands and are relatively free of insects and disease.

Each interior spruce cone could potentially produce about 200 seeds (Owens and Molder 1984). Up to 100 filled seeds per cone have been counted in local natural spruce stands. A conservative assumption as to the potential for filled seed production in a managed spruce seed orchard might be 90 seeds per cone. Using methods discussed by Bramlett and Godbee (1982), "seed efficiency" averaged over both the study years was only 18 percent ([16.1 seeds per cone realized - 90 seeds per cone potential] x 100). Supplemental mass pollination would be a useful tool to increase seed set.

Once we have the cones we must be able to harvest them. Flower and cone abortion losses of up to 75 percent of the crop have been observed for other species such as coast Douglas-fir (Pseudotsuga menziesii) (Bartram 1982). We don't know the magnitude of the losses for interior spruce.

In spite of the potential problems, our seed orchard managers should be able to meet our seed production goals. We know that transplanting shock substantially increases cone production. Our physiologists are attempting to duplicate these results in operational seed orchards using various combinations of root pruning, drought stressing (heat and water), GA 4/7 treatments, and fertilizing.

Table 2.--Cone production from 5-year-old transplanted interior spruce ramets

Variable	Ramets planted in 1981, data collected in 1984	Ramets planted in 1983, data collected in 1984
Seed orchard planning zone	Shuswap Adams	Shuswap Adams
No. of ramets	111	111
Avg. Ht. of ramets	140 cm	134 cm
Avg. no. of cones per ramet	2	88
No. of ramets > 100 cm in ht.	101	81
Avg. cone production per ramet < 100 cm	2.198	115.07
No. of ramets ≤ 100 cm in ht.	10	30
Avg. cone production per ramet ≤ 100 cm	0	14.9

In combination with booster pollination and insect and disease control we have the potential to exceed our seed production target. With a good quantity of genetically superior seed we are off to a good silvicultural beginning.

ACKNOWLEDGMENTS

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COLD STRATIFICATION FOR LODGEPOLE PINE SEED

A. K. Hellum and I. Dymock

ABSTRACT: In this study, cold stratification did not increase total germination of immature seeds (August) of lodgepole pine, had little effect on seeds at their peak of germination (September) and elicited no or negative responses from seeds frozen in fall before fully ripe (October). The germination rate was hastened consistently by cold stratification and the 42-day treatment lead to more rapid germination than did 21 days. The need for cold stratification apparently increases again as cones and seeds remain on the tree over winter.

INTRODUCTION

Cold stratification of tree seed implies temporary storage in a moist medium at temperatures just above freezing. This allows the breaking of dormancy (Copeland 1976) so that germination can proceed. Cold stratification is also done to allow after-ripening to take place (Edwards 1980) and it is accepted that seeds absorb moisture during this time or the treatment would serve no useful purpose. Seeds that cannot take up water do not respond to moist storage or cold stratification. The stratification is usually carried out for a minimum of 15 days for north temperate pines (Krugman and Jenkinson 1974) and must, in some species, last for up to 270 days.

Some authors claim that cold stratification is not needed for the full germination of lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) seeds from southern sources (Critchfield 1976) but it is considered as a basic need for more northern sources (Thompson 1984). It is carried out routinely on all lodgepole pine seeds used in nursery practice in Alberta. (See also Wheeler and Critchfield 1985).

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Our knowledge about what happens to seeds during cold stratification is incomplete (Tanaka 1984), but there is an understanding that if they are in need of cold stratification to germinate fully then they are not fully ripe (Edwards 1980). It is generally held that cold stratification is not harmful to germination of lodgepole pine seeds (Wang 1978).

In contrast, cold stratification normally hastens germination. The time to reach 50 percent of total germination may be shortened by days. Rapid germination in nurseries under controlled moisture conditions is a distinct advantage because it leads to the production of homogeneous crops of seedlings (Tinus and McDonald 1979). Spontaneous germination is an advantage and a requirement here, but it is certainly not desirable under variable field conditions. The need for cold stratification is therefore a built-in safety mechanism in seeds, which helps ensure that germination occurs at the right time in the field.

Cones of both spruce and pine can be collected soon after the embryo is fully developed, judging by x-ray photography, and provided the seeds are left in the cones for a month at about 10° C (50° F) and at about 65 percent relative humidity (Edwards 1978, 1980). The ripening which is taking place in such storage is therefore similar to that which takes place on the tree given that fall weather will allow this process to occur. Simak (1966), Kardell (1973), and Hellum and others (1983) have demonstrated that about 4 weeks are needed, after complete embryo development, before the seeds of Scots pine (*P. sylvestris* L.) and lodgepole pine reach their full germination potential.

The main purpose of this study was to test the relationship between seed ripening and the need for cold stratification. The effect of temporary cone storage before extraction was also investigated to evaluate the potential effects of after-ripening on need for cold stratification.

METHODS

The cones for this study were gathered from 20 felled trees at each of four collection times at three different altitudes (table 1) on the Procter & Gamble Cellulose (Canada) Ltd. lease area in the Grande Prairie forest of Alberta.

Table 1.--Lodgepole pine cone collections made south of Grande Prairie, Alberta, at four different times and three different altitudes between July and October 1984

Sample location	Altitude	Collection times	Total trees
	(m)		
54°55'N.,118°50'W. (Lower location)	670	July 17-20	80
		Aug 20-23	
		Sept 17-20	
		Oct 29-31	
54°38'N.,119°05'W. (Middle location)	970	July 17-20	80
		Aug 20-23	
		Sept 17-20	
		Oct 29-31	
54°25°N.,119°39'W. (Upper location)	1515	July 17-20	80
		Aug 20-23	
		Sept 17-20	
		Oct 29-31	

Cones collected in July 1984 represent the 1983 cone crop while cones collected in August to October represent the 1984 cone crop. Only trees with an estimated 30 cones or more of the desirable kind were felled. There were more trees without than with the required cones on these sites, so binoculars were used to assess each tree before felling. The 1984 cone crop was particularly poor at all three altitudes compared to 1983 and earlier crops.

Cones were kept separate by tree, site, and time of collection and seeds were extracted from 17 of the cones per tree, cleaned, and counted. The remaining cones were needed for other tests. The seeds were then pooled to make certain that the same number of filled seeds was pooled for each tree and stand per collection time. All germination tests were therefore run on fully balanced samples.

The cones were cracked open at 180° C (356° F) for about 3 minutes and then left overnight at 40° C (104° F) in a gravity vented kiln. Cones were then tumbled and seeds extracted, wet dewinged by hand, and cleaned in a North Dakota blower. The seeds were then left to air-dry for 24 hours and subsequently stored at about 3° C (37° F) until testing. Seed moisture contents were not measured after each collection trip and extraction and cleaning run because experience has shown seed moisture contents in general do not exceed 8 percent under similar conditions.

The cone moisture contents were determined within 48 hours of collection and five cones per tree, location, and collection time were dried at 105° C (221° F) for 24 hours. Moisture conditions were calculated on a dry-weight basis. Cones were dried intact without seeds being extracted first.

Eight cones were stored in paper bags in a cold room kept at 5° C to 10° F (41° F to 50° F) for 7 months from time of collection to test possible effects of after-ripening on seed dormancy. Four weeks should be long enough to satisfy after-ripening needs after which seeds should be able to withstand drying to 5 to 7 percent moisture. Seven months were used in this study due to work pressures.

The extraction, cleaning, and counting of seed took 4 weeks, and a maximum of 42 days of cold stratification was used. Thus, 70 days lapsed between collection and the onset of germination tests.

Cold stratification was done between layers of moist peat at 2° C for 21 and 42 days. Four replicates of 100 seeds were first x-rayed to determine empty and damaged seed counts for all tests. They were then placed on plastic frames 22 by 22 cm (8.8 by 8.8 inches) (approximately) which were covered with Kimpak and 1 cm of moist peat moss. The seeds were spread on top of the peat in four distinct replicates. These frames were stacked one on top of the other and all were covered with 2-mil plastic. These stacks, of about 20 frames, were opened only to remove frames to start the germination tests or to remoisten peat every 14 days.

Dry seeds (controls) were set to germinate at the same time as the 21-day and 42-day stratified seeds. The frames, Kimpak, peat, and seeds were placed in clear plastic boxes with lids and put in a Conviron germinator run at 30° C (86° F) during 8-hour days followed by 20° C(68° F) and 16-hour nights. Tests were terminated after the 21st day. Tap water was added as needed in mist form. The seeds were kept remarkably free of fungus or other pest problems.

Seeds were classified as germinated when the protruding radicle/hypocotyl was four times the length of the seed coat. The seeds were then removed. Cutting tests were not performed afterward because all replicates were x-rayed before tests started. Percent germination was therefore always calculated based on full seed only. Empty and damaged seed in these tests rarely exceeded 5 percent. Germination was counted daily at the same time.

The germination rate (R_{50}) is defined here as the time needed to reach 50 percent of the total germination of a sample. It was calculated in days for each replicate, source, and collection time by lineal interpolation on germination curves.

The radiographs were taken using 20 s exposures, 15 kV, 5mA (Milliampere) and a distance of 47 cm (18.8 inch). Seeds were put on top of the packaged film for exposing and films were then developed right away. This made it possible to make sure that no replicate used had more than about 10 percent empty or damaged seed.

RESULTS AND DISCUSSION

Cone Moisture Content

Average cone moisture contents dropped from about 60 percent of ovendry weight in mid-August to just over 20 percent in late October 1984 in all three sample stands regardless of altitude. This drying did not follow the expected concave asymptotic curve (Hellum and others 1983) observed earlier. It resembled more the right-hand part of a convex parabola showing very rapid moisture loss after rather than before the September collection (table 2). No doubt, the -20° C (-4° F) weather experienced just before the October collection affected cone ripening, but freezing tests on collected cones failed to yield useful data because the tetrazolium test was used to evaluate damages and this proved too unreliable. October was reportedly the coldest month in 30 years in Alberta.

Table 2.--Cone moisture contents for lodgepole pine at time of collection south of Grande Prairie, Alberta in 1984

Altitude of sample	Collection times (X ± 1SD)			
	July	August	September	October
(m)	1983 cones	1984 cones		
670	12.7±1.22	62.0±4.40	47.0±13.70	22.2±3.12
970	12.4±1.43	59.1±5.26	54.1± 7.18	21.8±2.56
1,515	12.8±1.44	62.5±6.09	59.3± 5.21	20.7±2.76

Natural cone drying proceeded most rapidly at the low site between August and September (15.0 percent) and slowest (3.2 percent) at the highest site. This trend was reversed between September and October. Now the cones at the highest site lost most moisture (38.6 percent) and the low site cones the least (24.8 percent). Judging by a study of 1980 cones from the same stands (Hellum and others 1983) the variability in cone moisture content should have been expected to be greatest during July and late September and least in August and in the following spring. The very rapid rates of cone drying from September to October 1984 are interpreted here as having been hastened by the -20° C (-4° F) temperatures and heavy snowfall experienced about 2 weeks before cone collection could proceed.

Coefficients of variation (table 3) suggest that tree-to-tree variability in cone moisture contents was greatest in the September collection at the low site and that August cones were quite homogeneous among trees at all altitudes. The October cones were only marginally more variable than the July cones of 1983.

The moisture contents for cones collected in July 1984, that is, cones ripened in 1983, were low (12.4 to 12.8 percent). They were between 7 and 9 percent lower than expected judging by a month-to-month survey done of cone moisture contents on the campus of the University of Alberta in 1982-1983 (Hellum unpublished). The cone moisture on campus dropped to about 15 percent in April and May in this period while it remained between 20 and 22 percent for the rest of the year. The low moisture values for July 1984 cones are interpreted as being indicative of very warm and dry forest conditions in the summer of 1984.

Table 3.--Coefficients of variation for data in table 2 on lodgepole pine cone moisture

Altitude of sample	Collection times (1984)			
	July	August	September	October
(m)	1983 cones	1984 cones		
670	9.5	7.1	20.1	14.0
970	11.5	8.9	13.3	12.1
1,515	11.2	9.7	8.8	13.3

Total Germination

Germination reached 92 percent and above for all seeds collected in September whether cold-stratified or not and regardless of location or altitude (fig. 1). The cold-stratified seeds did not reach higher levels of germination than the unstratified seeds. Seeds stratified for 42 days at 2° C (36° F) showed an average 3 percent less germination than those stratified for 21 days or not stratified at all (95 percent level of confidence).

Cold stratification at 2° C clearly damaged the high-altitude seeds collected in August (an 11.5 percent loss in total germination). The longer the cold stratification period the less germination obtained (99.9 percent level of confidence). No damages were observed in seeds collected at the mid and lower altitudes where seeds could reach 95-96 percent germination at this time.

Seeds collected in October, however, were significantly (95 percent level) less germinable (85.0 percent ± 5.5 percent) than those collected in September (95.2 percent ± 4.0 percent). Even though the seeds collected in August and September could germinate to above 90 percent the seeds collected in October never exceeded 85 percent and fell, on average, about 10 percent short of the September total. The -20° C (-4° F) temperatures in mid-October are assumed to have caused this 10 percent loss in total germination at all altitudes. It is surmised that the seeds from some trees, where cones dried more slowly, were more severely damaged than those from trees where cones had dried more rapidly (were more mature).

The cones from 1983, collected in July of 1984, showed clearly that cold stratification aided total germination in 1984 significantly (by 5 to 6 percent) at both the middle and higher altitudes (fig. 2). The trend was significant at the 99.4 percent level. The pretreatment did not influence total germination in seeds from the lower collection site. This response pattern agrees well with the 1984 cone data and the data from 1980 (Hellum and others 1983). It appears that an altitude of 670 m (2,211 ft) above sea level is low enough to allow relatively complete seed and cone ripening to occur before fall and winter frosts arrive.

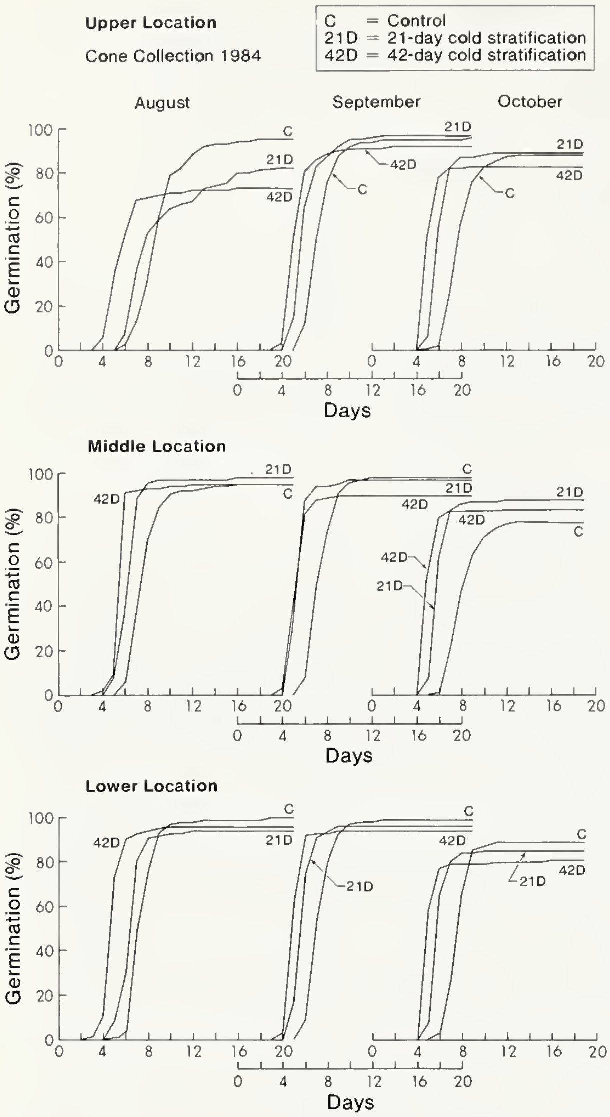

Figure 1.--Germination curves for seeds of lodgepole pine collected at three times and at three different altitudes in the Grande Prairie forest of Alberta. Seeds were cold-stratified for 21 and 42 days.

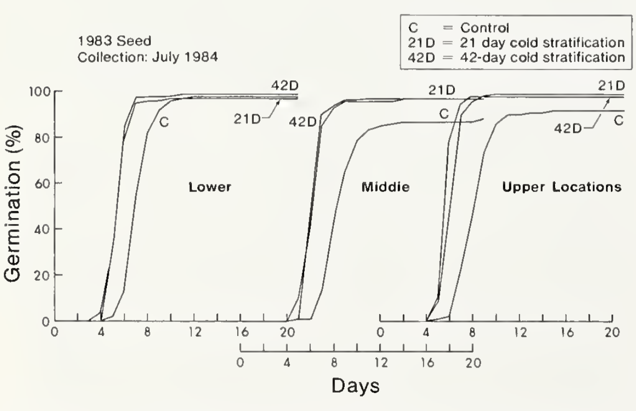

Figure 2.--Germination curves for 1983 lodgepole pine seed collected in July of 1984 from three different altitudes in the Grande Prairie forest of Alberta.

Germination Rate

Germination rates were improved significantly (99.9 percent level) with cold stratification compared to controls. The 42-day treatment gave significantly better (99.9 percent level), faster, germination (5.04 days ± 0.45) than the 21-day treatment (5.90 days ± 0.53) regardless of altitude of sample (fig. 1). The control took 7.49 days ± 0.53.

Seeds collected in September had the most rapid rate of germination (5.84 days ± 0.91), while the August seeds used 6.31 days ± 1.32 to reach the same point. The October seed was intermediate at 6.03 days ± 1.20. There was only a weak difference (significant at 90 percent level only) among germination rates over the collection period. The 1983 seeds, collected in July 1984, germinated to 50 percent in 6.40 days ± 1.03 and proved to be slower than the seeds collected in August and September, but the September seeds were similar to the October seeds (90 percent level of confidence).

The germination rate was therefore only slightly more rapid at the time when the 1984 seeds were ripest than before or after this time.

After-Ripening

Without exception, seed germination dropped significantly as a result of cone storage after August collection even though the relative humidity was maintained around 65 percent and temperatures kept at between 5 and 10° C (41 and 50° F). The attempted after-ripening led to a loss of over 31 percent germination at the lower altitude, 26.5 percent loss at the middle and 14.3 percent loss at the highest altitude site in August 1984. These losses were undoubtedly due to drying damages. A considerable proportion of the after-ripened seeds had cracked endosperms. Because after-ripening implies additional maturation such seeds should have been able to withstand long-term storage (7 months) without showing drying damages after the first 4 weeks.

The after-ripened seeds did not benefit consistently from cold stratification except in rates of germination. Total germination was sometimes

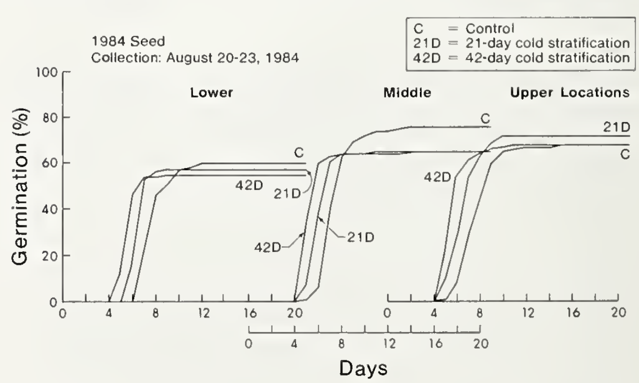

Figure 3.--Germination curves for after-ripened lodgepole pine seed collected in the Grande Prairie forest of Alberta in August of 1984.

slightly better in controls than in stratified seed and sometimes slightly worse (fig. 3). See also Winston and Haddon (1981).

CONCLUSIONS

In this 1-year study cold stratification hastened germination in lodgepole pine seeds. Cold stratification also elicited three kinds of responses in the same seed regarding total germination:

1. Immature (August) seeds were harmed by cold stratification at 2° C (36° F) and the longer the period of cold stratification the lower the total germination. The treatment effect was significant at the 95 percent level of confidence.
2. Once the seeds had reached their peak germination, which happened in late September in 1984, little or no additional germination could be obtained by cold stratification. In fact, the 42-day stratification had a slight negative effect on germination (99.3 percent level).
3. Seeds from 1983 (collected in July of 1984) benefitted by cold stratification and seeds collected in October 1984 could tolerate a 21-day period of stratification but not a 42-day period. It appears, therefore, as if seeds enter dormancy again gradually once winter sets it. There was a clear indication in these samples that altitude played a role.

A relative humidity of about 65 percent was not adequate for maintaining necessary cone moisture contents in order to allow after-ripening to proceed in lodgepole pine seed in this study.

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EFFECT OF STRATIFICATION TIME AND SEED TREATMENT ON GERMINATION OF WESTERN WHITE PINE SEED

R. J. Hoff

ABSTRACT: Germination of intact western white pine seeds increased from 7 percent for unstratified seeds to 83 percent for seeds that were stratified under cold-wet conditions for 15 weeks (105 days). Fifty percent of the seeds for which the seed coat and papery membrane were removed or pieces were cut away germinated with no stratification and 98 percent germinated after 15 weeks of stratification. Dormancy is determined mainly by the papery membrane and physiological elements of the embryo or gametophyte. The relative importance of these determinants changes with stratification time up to 105 days, after which only the papery membrane remains a barrier to the germination of about 15 percent of the seed. Families also had an impact on germination; family heritability of 79 percent was calculated.

INTRODUCTION

Cold-wet stratification has been the principal method for breaking dormancy in western white pine (Pinus monticola) seed. And yet high germination was seldom assured. Germination sometimes would be high, other times low; worst of all, there was no predictability even when the seed could be shown to be viable, for example by using seed cutting tests (Hoff and Steinhoff, in press).

Several kinds of treatments have been tried; for instance, alternating cold and warm stratification, acid soak, freezing, cutting, scarification, sodium hypochlorite soak, long-term soaking in water, and infrared light exposure (Larsen 1925; Anderson and Wilson 1966; Partridge and others 1985; Works and Boyd 1972; Malone 1983) have been used with variable success.

The objectives of this research were to 1) determine the effect of stratification time on germination when physiological ripeness of cones and conditions of stratification were closely controlled; 2) to assess the interactions with length of stratification of various seed treatments involving the removal of or cutting of the seed coat and papery membrane; and 3) to assess the impact of families on germination.

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METHODS AND MATERIALS

The seeds came from 20 individual trees (families) located in the Palouse River drainage, ID, latitude 46°59'N, longitude 116°33'W., elevation 823 m (2,700 ft). Cones were harvested from individual trees when they had become flaccid--the cones were no longer hard and they could be bent back and forth with little or no crackling. In this state the cones had not dried very much, but the scales were no longer stuck to each other. All cones were picked within 7 days in September 1984. Cones were dried in a greenhouse, seeds were extracted and then stored at 3 °C (37 °F). Seed germination tests were started November 1984.

Five hundred seeds of each family were placed in a small plastic mesh bag; seed surfaces were sterilized in a 0.25 percent sodium hypochlorite solution for 10 minutes. Seeds were rinsed three times with water and then given a 24-hour running water rinse.

The seeds were then subjected to five seed treatments and five stratification times: 0, 21, 42, 90 and 105 days.

To stratify, each of the 20 family seed lots was rolled up in a wet paper towel and placed in an unsealed small plastic bag. An insulated box inside a refrigerator was used as a stratification chamber and temperature was monitored remotely. Stratification temperature was maintained at 3 °C ±1 (37 °F ±1).

After each stratification time the seeds were subjected to five treatments:

1. Seeds intact (fig. 1A).
2. A part of the seed coat was carefully removed so as not to damage the membrane that lies between the seed coat and gametophyte (fig. 1B).
3. The entire seed coat was removed. Because the membrane is attached to the seed coat at both ends of the seed, part of the membrane was also removed (fig. 1C).
4. A slice was cut out of the seed. This cut included the seed coat, membrane, and a small part of the gametophyte (fig. 1D).
5. The tip (radicle end) of the seed was cut off. This could be only 1-2 mm (1/16-inch) from the tip so as not to cut the radicle or at least to minimize cutting it (fig. 1E).

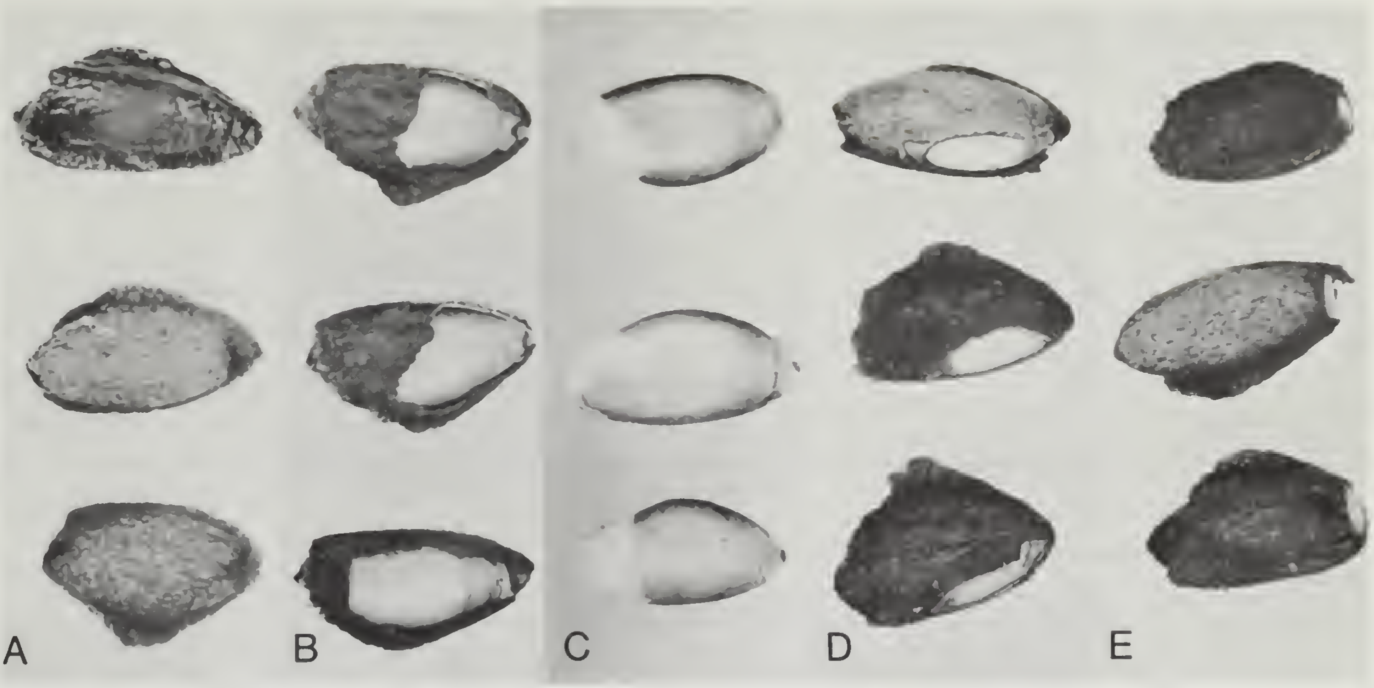

Figure 1.--Western white pine seed treatments: A, intact; B, part of the seed coat was removed leaving the papery membrane intact; C, all of the seed coat was removed which tore part of the membrane away with it; D, seed was cut on the side, cutting through the seed coat, membrane, and into the gametophyte; E, the tip (radicle end) was cut, cutting seed coat, membrane, and a very small piece of the gametophyte. (magnification = 7x)

The seeds were incubated in 6-cm (2.4-inch) plastic petri dishes containing two filter paper pads that were kept moist. Each test was laid out on a laboratory bench maintained at 20 °C (68 °F). Germination data were taken 21 days after incubation began. A seed was counted as a germinate when the radicle had grown at least one-half the length of the seed.

The analysis of variance and expected mean squares are shown in table 1. The model assumes that treatments are fixed and stratification time and families are random. Before analysis, the data were transformed to arcsin$\sqrt{\%}$ and differences among treatment and stratification means were determined with Duncan's New Multiple Range Test (Steel and Torrie 1960).

Table 1.--Model for analysis of variance and expected mean squares

Source of variation	Degrees of freedom	Expected mean squares[1]
Block	1	$\sigma_e^2 + tsf\sigma_b^2$
Treatment (trt)	4	$\sigma_e^2 + b\sigma_{tsf}^2 + bs\sigma_{ts}^2 + bf\sigma_{ts}^2 + bsf\sigma_t^2$
Stratification time (str)	4	$\sigma_e^2 + bt\sigma_{sf}^2 + btf\sigma_t^2$
Families (fam)	19	$\sigma_e^2 + bt\sigma_{sf}^2 + bts\sigma_{ts}^2$
Trt x str	16	$\sigma_e^2 + b\sigma_{tsf}^2 + bf\sigma_{ts}^2$
Trt x fam	76	$\sigma_e^2 + b\sigma_{tsf}^2 + bs\sigma_{tf}^2$
Str x fam	76	$\sigma_e^2 + bt\sigma_{sf}^2$
Trt x str x fam	304	$\sigma_e^2 + b\sigma_{tsf}^2$
Error[2]	499	σ_e^2

[1]Where: b = 2, t = 5, s = 5, f = 20.

[2]Contains all sources of variance involving interactions of blocks.

Table 2.--Average percentage germination of seed from 20 families of western white pine after various treatments and stratification times

Seed treatment	Days of cold-wet stratification					
	0	21	42	90	105	Mean
Intact	7	36	44	81	83	50
Seed coat cut - membrane intact	16	33	47	81	84	50
Seed coat removed - membrane broken	49	61	69	98	98	75
Side of seed cut - membrane cut	50	62	77	94	99	76
Tip of seed cut - membrane cut	51	62	71	94	99	75
Mean	35	51	62	89	93	66

Family heritability was calculated using the formula:

$$h^2 = \frac{\sigma^2_f}{\sigma^2_f + \frac{\sigma^2_{sf}}{s} + \frac{\sigma^2_e}{bts}}$$

RESULTS

An increase in cold-wet stratification time resulted in an increase in germination for all seed treatments (table 2). This varied from 35 percent for no stratification over all treatments to 93 percent after 105 days' stratification. These means were significantly different at the 1 percent level of probability (table 3). Stratification time accounted for 54 percent of the variation.

Results of Duncan's New Multiple Range Test of the germination means for stratification time were:

	Stratification time				
	0 days	21 days	42 days	90 days	105 days
$\bar{x}$ germination	35	51	62	89	93

Means underscored by the same line are not significantly different at the 5 percent level of probability.

The effect of seed treatment is also shown in table 2. These means were significantly different at the 1 percent level of probability (table 3). Treatments accounted for 14 percent of the variation. Duncan's test at the 5 percent level of probability indicated that treatments 1 and 2 (seed coat intact and membrane intact) were not significantly different and that treatments 3, 4, and 5 (those that disrupted the seed coat and membrane either by removal or cutting) also did not differ, but that these two groups differed.

Table 3.--Analysis of variance and variance components for percent germination of western white pine seed

Source of variance	Degrees of freedom	Mean square	Variance component	Percent of variance
Block	1	0.008	-.000	--
Treatment (trt)	4	6.881**	.033	14
Stratification time (str)	4	25.827**	.129	54
Families (fam)	19	0.675**	.012	5
Trt x str	16	0.202**	.004	2
Trt x fam	76	0.118**	.006	3
Str x fam	76	0.082**	.005	2
Trt x str x fam	304	0.056**	.010	4
Error	499	0.036	.036	15

**Statistically significant at the 1 percent level of probability.

Treatments 3, 4, and 5 averaged 50 percent germination with no stratification compared to 12 percent for treatments 1 and 2. The differences in seed treatment decreased with stratification time. But still, at 105 days' stratification, germination of the seeds with intact coats and membranes had not equaled that of seeds whose coats and membranes were disrupted.

Seed lot also had a significant effect on germination (table 3). Table 4 combines treatments 1 and 2 and shows the frequencies of family germination means for each stratification time. Intact seeds from two trees had more than 30 percent germination with no stratification, and there were two other trees with very low seed germination, even after 105 days' stratification. Nearly 100 percent of the seeds of all four of these trees germinated after 105 days' stratification when the seed coats and membranes were disrupted.

Table 5 combined treatments 3, 4, and 5 to show frequencies of family germination means for each stratification time. The lowest average germination was 22 percent for no stratification and the highest was 75 percent. After 105 days, the lowest germination was 92 percent.

Family heritability was:

$$h_f^2 = \frac{.012\ (.90)}{.012 + \frac{.005}{5} + \frac{.036}{50}} = .79$$

Additive genetic variation was decreased by 10 percent to account for average inbreeding in natural stands.

Table 4.--Frequency of average germination by family for each stratification time for treatments 1 and 2[1]

Percent class	Days of stratification				
	0	21	42	90	105
1-10	11	1	1		
11-20	7	3	2		
21-30		6	2	1	1
31-40	2	3	4		
41-50		4	3		1
51-60		3	4	1	
61-70			1	3	2
71-80			1	2	2
81-90			2	5	5
91-99				5	6
100				3	3

[1]Treatment 1 = seed coat intact, treatment 2 = membrane intact.

Table 5.--Frequency of average germination by family for each stratification time for treatments 3, 4, and 5[1]

Percent class	Days of stratification				
	0	21	42	90	105
1-10					
11-20					
21-30	2	1			
31-40	3				
41-50	2	3			
51-60	7	4	5		
61-70	5	7	4		
71-80	1	5	4		
81-90			6	2	
91-99			1	15	7
100				3	13

[1]Treatment 3 = seed coat and part of membrane removed, treatment 4 = seed coat and membrane cut, treatment 5 = seed tip cut.

DISCUSSION

The effect of stratification time was obvious and expected. But still 105 days were not enough to overcome all the components of dormancy for the intact seed. Seeds from two trees had rather low germination (30 and 42 percent) after 105 days' stratification, and nearly every seed lot had some seed that did not germinate after 21 days' incubation. Cutting these ungerminated seeds after 21 days' incubation resulted in rapid germination. Thus, these seeds were physiologically viable.

Considering the various seed treatments together with stratification time reveals some of the "sites of dormancy." With no stratification, 7 percent of the intact seed germinated; 16 percent germinated with an intact membrane; and 50 percent of the seed with disrupted seed coat and membrane germinated. Interpretation in terms of dormancy indicates that 7 percent had no dormancy, 9 percent (16-7) had seed coat dormancy, 34 percent had dormancy due to the papery membrane (50-16), and 50 percent (100-50) had physiological elements in the embryo, gametophyte, or both, that prevented germination. Even though Duncan's test indicated that the intact seed and intact membrane treatments did not differ at all stratification times, it is possible that they do with no stratification, and thus they were kept separate. The treatments that disrupted the seed coat and membrane were averaged for each of the stratification times. Table 6 shows the proportional change of these sites of dormancy over stratification time.

Table 6.--Change in percentage of western white pine seed with no dormancy, with seed coat, membrane, and physiological dormancy for five levels of cold-wet stratification

Site of dormancy	Days of cold-wet stratification 0	21	42	90	105
	Percent				
None	7	35	44	81	84
Seed coat	9	0	0	0	0
Membrane	34	22	6	14	15
Physiological	50	38	28	5	1

Physiological dormancy has probably been overcome by 90 days' stratification and possibly much earlier--sometime between 42 and 90 days. Seed coat dormancy appears to be eliminated by about 21 days of stratification. Thus, the main element of dormancy that is present after 90 and 105 days involves the papery membrane.

The membrane or seed coat do not appear to be physical barriers, because seeds that are physiologically ready to germinate and that are inhibited by the seed coat/membrane will readily germinate through the seed tip (normal area for emergence of the radicle) when the seed is cut on the side. These structures are most likely to be barriers to water or gas exchange. For some trees, the seed coat/membrane is thought to be a barrier to oxygen transport (Stone 1957; Kozlowski and Gentile 1959).

That seed germination is strongly influenced by family is indicated by the high heritability. To assure equal representation of all families in a particular seed lot, seeds of each family should be kept separate, given the specific treatment needed to break dormancy, sown separately, and then combined after the seeds have germinated.

CONCLUSIONS

1. Cold-wet stratification resulted in high germination for most seed lots, but 105 days were not enough for some seed lots.
2. Disrupting the seed coat and membrane will result in moderate germination even without stratification.
3. The sites of dormancy observed were: seed coat, papery membrane, and physiological elements of the embryo, gametophyte, or both.
4. Family heritability was high (0.79) indicating a substantial genetic component.

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SEED DORMANCY IN THREE PINUS SPECIES OF THE INLAND MOUNTAIN WEST

Carole L. Leadem

ABSTRACT: Several seed sources of Pinus albicaulis, Pinus contorta, and Pinus monticola were given various treatments to determine the degree and type of dormancy restricting germination in each species. The occurrence of physiological and mechanical dormancy was investigated using stratification (moist chilling at 2°C) and partial removal of the seedcoat. Development of embryo and gametophyte tissue was assessed using X-rays. Where incomplete development was suspected, a combination of warm (20°C) and cold (2°C) stratification was also employed.

Physiological dormancy, measured as the degree of response to various stratification periods, was greatest in P. albicaulis and P. monticola, and least in P. contorta. Seed coats imposed significant restraints to radicle protrusion in P. albicaulis and P. monticola, but only slightly affected germination of P. contorta. Germination of P. albicaulis is also commonly restricted by seed immaturity due to short growing seasons found in subalpine regions.

The results are discussed with regard to the dormancy strategies and the habitats in which each of the species is generally found.

INTRODUCTION

Seeds are said to be dormant when they are placed under conditions favourable for growth, yet fail to germinate. Dormancy, found in most tree seeds, is an important adaptive mechanism because it ensures the survival of the species by delaying germination until conditions in the external environment are conducive to active growth (Osborne 1981). The expression of dormancy is under genetic control (Naylor 1983), but it is also strongly influenced by environmental factors (Steinhoff and others 1983; Rehfeldt 1983, 1985). Through variations in environment, plant populations become physiologically specialized to segments along the environmental gradient. Dormancy is part of the life strategy by which species adapt to the local environment. Since the most successful species are those which are most suited to a particular habitat, specializations in the manner by which dormancy is controlled result in a more successful life strategy. Control of dormancy can be exerted exogenously by physical, chemical, or mechanical means, but can also be achieved endogenously via morphological or physiological traits (Nikolaeva 1977). The type of control varies by species, even within members of the same genus.

Pinus albicaulis Engelm., Pinus contorta var. latifolia Engelm., and Pinus monticola Dougl. are three pines found primarily in mountainous areas throughout the western United States and Canada (fig. 1). P. albicaulis (whitebark pine) is a subalpine species common at high elevations growing in shallow soils on exposed slopes and rocky ridges. Climatic conditions are characterized by cool summers and cold winters with deep winter snowpack. Trees have high frost resistance but low shade tolerance (Krajina 1969; Franklin and Dyrness 1973). P. contorta (lodgepole pine) is an extremely adaptable tree which occurs in habitats from dry forest to swamp, and from lowlands to subalpine. Climatic requirements are also wide, but shade tolerance is almost nil, even in the driest habitats (Krajina 1969). It is usually considered a pioneer species, although it can be a persistent seral or climax species under certain conditions (Volland 1985). P. monticola (western white pine) is a relatively diverse species growing anywhere from mesic forests to swamps and bogs. It is found in lowlands, but is also well adapted to interior montane areas. Trees are moderately shade tolerant, but are not very frost resistant. P. monticola requires at least 50 cm precipitation in the interior and 100 cm along the coast (Krajina 1969).

Figure 1.--a; cone lengths, clockwise from left, P. monticola (13-20 cm), P. contorta (2-6 cm), and P. albicaulis (4-8 cm), b; seed lengths, left to right, P. albicaulis (8-13 mm), P. monticola (5-8 mm), and P. contorta (3-4 mm).

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The three species can occur sympatrically (Sowell and others 1982), but in zones where they coexist, such as the Abies lasiocarpa zone of Oregon and Washington, P. monticola tends to be distributed lower in the zone, whereas P. albicaulis is conspicuous higher in the zone (Franklin and Dyrness 1973). In addition to their distribution along environmental clines, there are indications that these three species have variable requirements for breaking seed dormancy (Anderson and Wilson 1966; Pitel and Wang 1980; Hellum and Wang 1985). The questions to be addressed in this study are how dormancy mechanisms vary among closely related members of the same genus, and if control of dormancy can be related to their habitat of origin.

MATERIALS AND METHODS

Pinus albicaulis Engelm.

In 1981 and 1982 P. albicaulis seeds (lots P81 and P82) were collected from a small stand of trees on Baker Mountain (latitude 49°28', longitude 115°38', elevation 2200 m) near Cranbrook, British Columbia. Seeds were X-rayed prior to treatment to remove empty seeds and to assess gametophyte and embryo development. For experiments in which they were sterilized, seeds were soaked for 5 minutes in a 4% solution of sodium hypochlorite (NaOCl), rinsed three times with deionized water, then soaked for 48 h in fresh deionized water. Cold stratification to release seeds from physiological dormancy was conducted at 2°C for either 30 or 60 days, as indicated in tables 1 and 2. Compound stratification was used to promote development and break dormancy of immature seeds. In compound stratification seeds receive 30 or 60 days warm stratification at 20°C followed by 30 or 60 days stratification at 2°C.

For germination tests seeds were incubated for 30 days at 20°C with continuous light (Pitel 1982). Four replications of 25 seeds each were used for each treatment. In instances where seeds were clipped, 1 mm of the seedcoat was cut from the radicle end just prior to incubation. Data were analyzed by Analysis of Variance and differences between treatment means were determined using Duncan's Multiple Range Test.

Imbibition studies were performed on 20-seed samples soaked in deionized water at 20° C. Water uptake was determined from the means of four samples which were weighed at 0, 1, 2, 4, 8, 24, 48, 72, and 96 h after the start of soaking. Moisture content (m.c.) on a fresh weight basis was calculated after seeds had been dried for 24 h at 105°C. Determinations were made on a total of three southern B.C. interior seed sources (including P82).

Pinus contorta Var. latifolia Engelm.

Seeds were obtained from four seed sources collected in the interior of B.C. between 1967 and 1973.

Prior to germination testing, seeds were soaked for 24 h and stratified for 3 wk at 2°C. Seeds were incubated at 30°C/20°C with 8 h light for 3 weeks. Four replications of 100 seeds were used for each treatment. Germination data were analyzed and water uptake was measured as described for P. albicaulis.

Pinus monticola Dougl.

Three southern B.C. interior seed sources collected in 1964 and 1977 were used for experiments. To determine the most effective means of breaking dormancy, seeds were soaked for 24 h, then given five treatments: (1) stratification at 2°C for 60 days, (2) stratification at 2°C for 90 days, (3) stratification-redry, i.e., stratification for 30 days at 40% m.c., followed by 90 days at 30% m.c., (4) stratification for 0 days, (5) stratification for 30 days at 20°C, followed by 60 days at 2°C. To ascertain the degree of mechanical restraint imposed by the seedcoat, all stratification treatments were combined with a seedcoat treatment. Either 1 mm of the radicle end of the seed coat was cut off, or the coat was left intact. After stratification and seedcoat treatments, seeds were incubated at 30°C/20°C for 3 weeks with 8 hours light during the high temperature period. Four replications of 100 seeds were used for each treatment, and data were analyzed as for P. albicaulis. Water uptake was measured as described for P. albicaulis.

RESULTS

Pinus albicaulis

Morphological dormancy, defined by Nikolaeva (1977) as under-development of the embryo, was clearly evident in P. albicaulis. Embryo and gametophyte tissue incompletely filled the seeds prior to treatment (fig. 2a), but maintaining imbibed seeds under warm conditions for 30 to 60 days effectively promoted development of the immature tissue. This was visually demonstrated in X-rays taken following stratification (fig. 2b) and by results of germination tests (table 1).

The effects of cold temperatures on germination also indicated the presence of physiological dormancy. Warm temperatures enhanced seed development, but seeds still required an additional 60 days at 2°C to break dormancy (table 1). However, it was first necessary to remove mechanical restraint by clipping the coats, for even with the longest compound stratification, only 4% of the seeds

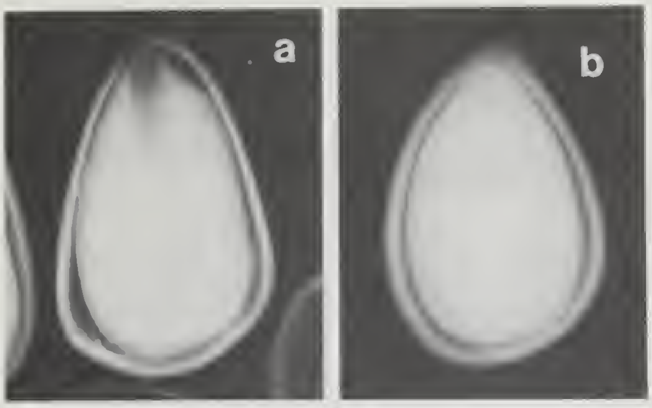

Figure 2.--Seed development of Pinus albicaulis as determined by X-ray. (a) prior to treatment (b) after 30 days at 20°C plus 60 days at 2°C.

with intact coats were able to germinate. A high incidence of microbial growth was noted in all treatments during the first test, so a second experiment was devised to examine if surface sterilization would reduce mold and thus improve germination. Seeds were sterilized, rinsed, and imbibed for 48 h prior to receiving either 60 days cold, or 60 days warm plus 60 days cold stratification. All coats were clipped prior to incubation to remove mechanical restraint. Sterilization only slightly increased germination of seeds which received cold stratification, but significantly improved germination of seeds which received the combined warm and cold treatment (table 2). Mold was still apparent during testing, but in view of the gains made in germination, sterilization was continued as the standard procedure.

A third experiment was performed to see if there was any benefit to modifying the procedure by completely removing the seed coat. Seeds were sterilized, then stratified using the combined warm and cold treatment. After stratification, coats were either left intact, clipped, or removed. In intact seeds, germination was 8%, but both seedcoat treatments resulted in higher emergence (table 3). There was apparently no advantage to removing the coat, since germination was about 30% regardless of whether the coat was clipped or entirely removed.

P. albicaulis is a hard-coated pine seed, but coats did not appear to be impermeable to water. Early water uptake was rapid, reaching 30% m.c. within 24 h, but seeds were not fully imbibed even after 96 h (fig. 3).

Pinus contorta

Most British Columbia sources of P. contorta will germinate moderately well without stratification. However, stratification usually increases both germination rate and total germination, so chilling for three weeks at 2°C is commonly recommended (International Seed Testing Association 1976).

Table 1.--Effects of clipping and stratification on germination of Pinus albicaulis (Lot P81)

Treatment			Germination percent
Days @ 20°C	Days @ 2°C	Clipping	
0	60	-	0.0
0	60	+	0.0
30	30	-	0.0
30	30	+	0.0
30	60	-	0.0
30	60	+	8.0[b]
60	60	-	4.2[b]
60	60	+	30.0[a]

Germination after 30 days incubation at 20°C with continuous light. None of the treatments was sterilized prior to treatment. Means with the same letter are not significantly different at p=0.05.

Table 2.--Effects of sterilization and stratification on germination of Pinus albicaulis (Lot P82)

Treatment				Germination percent
Days @ 20°C	Days @ 2°C	Ster.	Clip	
0	60	-	+	6.7[c]
0	60	+	+	9.9[c]
60	60	-	+	20.2[b]
60	60	+	+	31.4[a]

All seeds were clipped at the radicle end just prior to incubation. Seeds were incubated for 30 days at 20°C with continuous light. Percentages followed by the same letter are not significantly different at p=0.05.

Table 3.--Effects of the seedcoat on germination of stratified P. albicaulis seeds (Lot P82)

Treatment	Germination percent
Intact coat	8.0[b]
Clipped coat	32.2[a]
No coat	30.0[a]

All seeds were surface sterilized, then stratified for 60 days at 20°C plus 60 days at 2°C. Incubation was for 30 days at 20°C with continuous light. Means with the same letter are not significantly different at p=0.05.

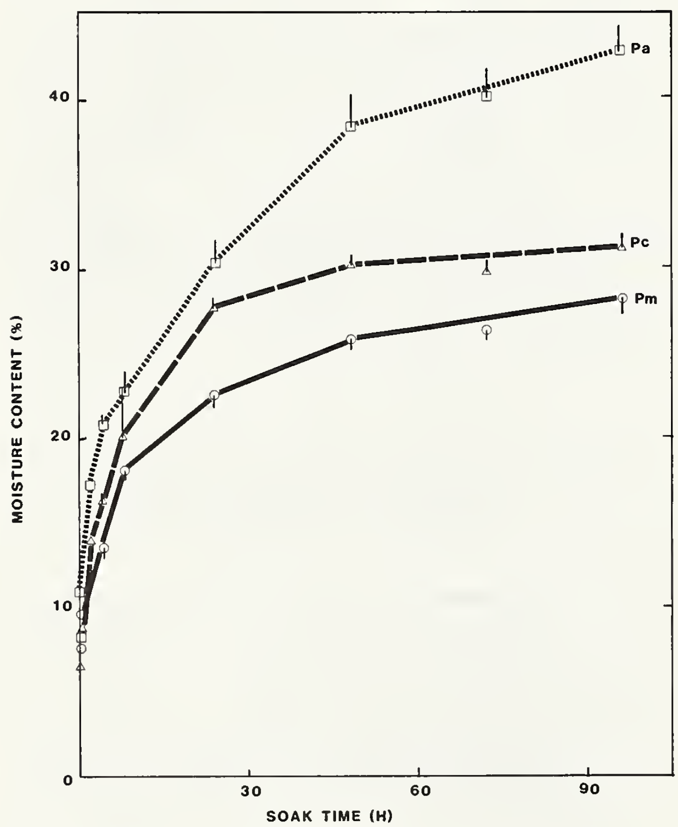

Figure 3.--Moisture content of P. albicaulis, P. contorta, and P. monticola seeds as affected by length of imbibition: □ P. albicaulis, △ P. contorta, ○ P. monticola. Data points are based on the means of 12 separate moisture determinations. Note that only half of the standard error bar is shown for each point.

To assess the degree of dormancy in P. contorta, stratified seeds were compared to unstratified controls. Mean germination of the stratified and unstratified seeds was not significantly different, indicating that physiological dormancy was not present in the lots used in this study.

Generally, it would be expected that germination of clipped seeds by removal of mechanical restraint would be the same or slightly higher than that of intact seeds, but cutting the seeds decreased average germination from 60% to 42% (table 4). Cutting the seeds not only destroyed the integrity of the coats but probably damaged the seeds in other ways, although mold was not a problem in intact seeds, substantial fungal growth was present on seeds which had been clipped.

Seedcoats of P. contorta do not appear to mechanically restrict germination, nor do they act as a barrier to water. A study of the water uptake performed on three seed sources showed that seeds were almost completely imbibed within one day (fig. 3). Seeds reached 28% m.c. during the first 24 h and gained only an additional 3% m.c. during the remainder of the 96 h period.

P. monticola

Relative to unclipped controls, clipping the seedcoats increased germination from 10% to 40% (fig. 4). On average, unstratified seeds germinated only 8% without clipping, but about 38% with clipping.

Table 4.--Effects of clipping and stratification on germination of P. contorta

Seedlot	Germination percent + Strat - Clip	- Strat - Clip	- Strat + Clip
1427	54.3[a]	54.5[a]	45.5[a]
1806	62.0[a]	60.3[a]	36.3[b]
2112	57.8[ab]	68.5[a]	42.5[b]
2238	59.8[a]	57.5[a]	41.5[b]
MEAN	58.5	60.2	41.5

Seeds were soaked for 24 h, stratified for 3 wk at 2°C, and incubated at 30°C/20°C with 8 h light for 3 wk. Means with the same letter are not significantly different at p=0.05.

Stratification consistently increased germination capacity but the degree of response varied with the treatment and seed source. For lot 633, stratification for 60 days at 2°C was most effective, but for lots 849 and 3249, the best treatment was 90 days at 2°C. For stratified and clipped seeds, germination was 73%, 82%, and 92% for lots 633, 849, and 3249, respectively.

The two alternate stratification techniques were less effective than the standard method. In the stratification-redry technique (treatment 3), moisture is controlled during stratification by chilling seeds for 30 days at 40% m.c., then for 90 days at 30% m.c. (Danielson and Tanaka 1978). This treatment has proven effective in releasing *Abies* species from dormancy (Edwards 1982; Leadem 1985). However, performance of *P. monticola* was very poor using this treatment, averaging only about 10% germination (fig. 4). It appears that the redry method either requires some modification before being applied to *P. monticola*, or alternately, is entirely unsuitable for breaking dormancy of these seeds.

Compound stratification was included because it is frequently used for immature seeds to enhance embryo growth, however, when tested on *P. monticola*, germination was usually not greater than that of unstratified seeds (fig. 4). However, response to a stratification method promoting embryo growth was not expected, because embryos appeared to be fully elongated in X-rays taken prior to treatment.

Although seed coats imposed a significant obstacle to radicle protrusion (fig. 4), they did not constitute an appreciable barrier to water uptake (fig. 3). Water uptake by *P. monticola* seeds, although less than the other two pines, was virtually complete within 48 h. Moisture contents of intact seeds which averaged 26% at 48 h had only increased to 28% by 96 h.

DISCUSSION

Seed immaturity, as well as physiological dormancy, was responsible for the poor germination of *P. albicaulis*. Because the species is found at high elevations, the

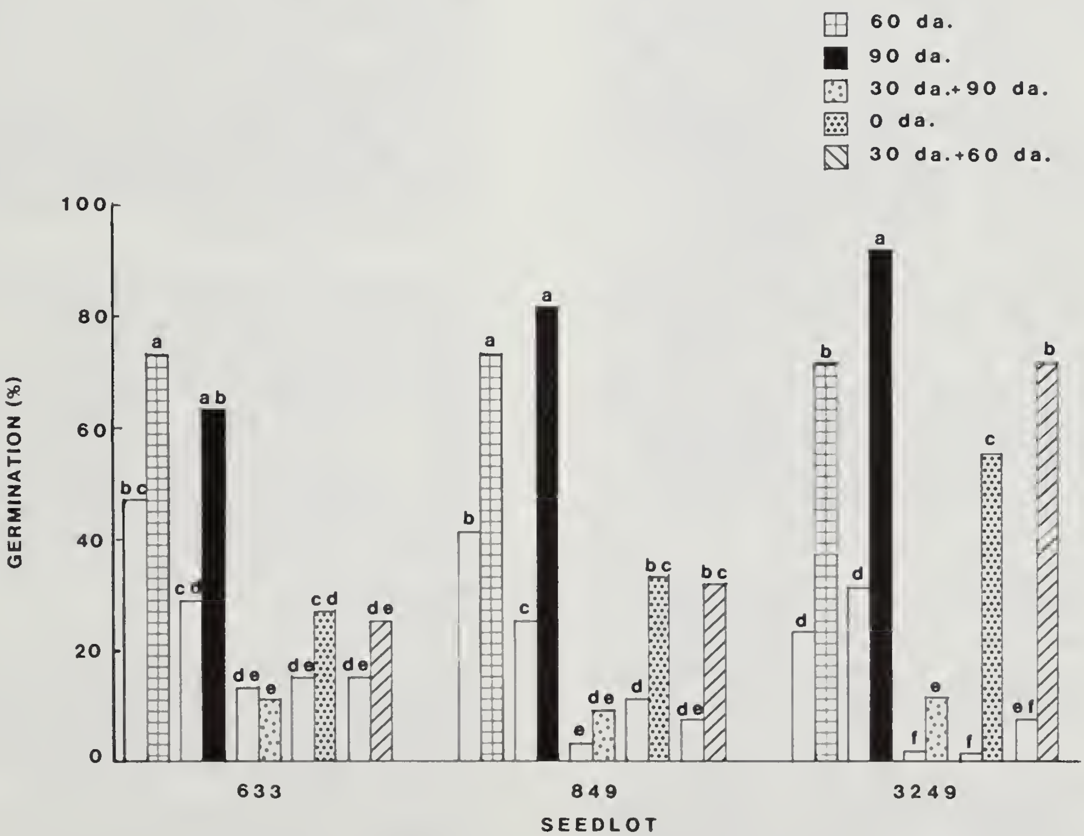

Figure 4.--Effects of clipping and stratification on germination of *P. monticola*. Stratification treatments are in order as follows: 60 days at 2°C; 90 days at 2°C; 30 days at 40% m.c., followed by 90 days at 30% m.c.; 0 days at 2°C; 30 days at 20°C, followed by 60 days at 2°C. Black and hatched or dotted treatment bars represent germination of clipped seeds, while blank bars are corresponding percentages for intact seeds. Data points are means of six 100-seed replicates. Means with the same letter are not significantly different at p=0.05.

growing season may be limited to a few months, leaving very little time for seeds to mature in the cones. Also contributing to poor development is premature harvesting by the Clark's nutcracker and small rodents such as chipmunks and squirrels. P. albicaulis cones are indehiscent, lacking the tracheid cells which in other pines cause scales to reflex and release the seeds (Lanner 1982). Thus, seed dispersal is dependent upon the dissection of cones by animals foraging for food (Tomback 1981). Unfortunately, foraging animals are not concerned with embryo development and will harvest seeds long before they are mature. As a result, it is often necessary to harvest cones while they are immature to ensure that they are still intact.

The lack of development in P. albicaulis was partially overcome by exposing imbibed seeds to 20°C to enhance embryo elongation, but warm temperatures alone were inadequate to effect dormancy release. Seeds required at least 60 days of cold temperatures (2°C) to overcome physiological barriers to growth. Clipping the seedcoat was also a necessary prerequisite for germination. However, the fact that clipping was necessary indicates that stratification treatments did not fully satisfy the germination requirements of P. albicaulis. Although clipping is considered a measure of mechanical restraint, I feel that mechanical and physiological dormancy are not separate entities. Rather, dormancy should be considered a single phenomenon representing a balance between the mechanical constraint of the coat and the expansive force of the embryo (Chen and Thimann 1966; Barnett 1972). Stratification is an effective dormancy-breaking technique which initiates metabolic processes that may alter the outer seed layers and increase the growth potential of the embryo. It is this increased growth capacity, and to a lesser degree a weakening of outer tissues, which enables the embryo to rupture the seedcoat and germinate. It should be noted that increased growth capacity was not verified in this study because embryo growth tests were not performed. How stratification affects growth potential may be explored in future studies.

The P. contorta lots employed in this study did not exhibit dormancy since unstratified seeds germinated as well, although not as quickly, as stratified seeds. The seedcoat did not prevent radicle emergence, nor did it restrict the entry of water.

For P. monticola, the failure to germinate appeared to be primarily due to physiological dormancy because all three lots used in this study responded best to stratification conducted at 2°C for 60 to 90 days. Two modified stratification techniques were tested in addition to the above methods: combined warm/cold stratification, which is often beneficial for enhancing germination of immature seeds, and the stratification-redry method, which has been shown to be successful when extended stratification periods must be used to overcome dormancy. However, neither of these alternate methods were as effective as the standard stratification treatment at 2°C. A strong component of dormancy seemed to be the restraint imposed by the coat, since clipping the seedcoats increased germination regardless of the type of stratification used. As with the other two pines, seedcoats only affected protrusion of the radicle and did not constitute barriers to water. Thus, as noted earlier, it is not the inability of the seeds to imbibe water which is responsible for lack of germination, but other physiological factors which prevent rupture of the coat.

How can the preceding observations be related to what is known about the habitats and life strategies of the three pines? P. albicaulis is a species which is able to survive in marginal subalpine habitats with short growing seasons. The lack of seed wings and indehiscence of the cones has resulted in dependence on animals for dispersal of the seeds. Seeds frequently do not mature on the tree during the short growing season, but the caching of the seeds in the soil by animals allows the seeds to continue ripening during long storage under the snow. X-ray evidence and results from germination tests reveal large variability in seed development and dormancy. These traits would suit a life strategy whereby only a few individuals germinate at a time so that all regeneration efforts do not occur at once, in the event that conditions are unfavourable. This strategy may be conservative, but is more likely to ensure continuation of the species in a harsh environment.

P. contorta is a pioneer species which is opportunistic in nature. Although it can be found anywhere from dry to wet sites, it is generally a shade intolerant species which starts to decline in importance once the canopy begins to close. As a prominent member of the initial seral stage of ecosystems in which it is found, it must germinate quickly to fill the pioneer niche. Therefore, most seed populations of P. contorta tend not to be dormant. For this species, there would be little advantage to delaying germination since habitats would tend to become less favourable with time.

P. monticola is a widespread species found in mesic environments of the western United States and Canada. Relative to P. albicaulis and P. contorta, P. monticola exists in a stable environment where water, temperature, and shade conditions are generally favourable. There is no necessity for rapid germination, nor must germination be extended over a long period, thus dormancy is probably governed by other factors.

The results of this study indicate that the type of dormancy exhibited by seeds of P. albicaulis, P. contorta and P. monticola can be related to their habitat of origin.

Each species occupies a different ecological niche, and as life strategies vary according to changes in local environments, so would dormancy control mechanisms also be expected to differ. The data show that dormancy does vary between species, although the release mechanisms are presently unknown. The nature of these mechanisms may be difficult to determine because of the variable responses to stratification as shown, for example, by different seed sources of P. contorta (Kamra 1982; Hellum and Wang 1985). Notwithstanding these difficulties, understanding the control of dormancy in coniferous seeds would have significant impacts in both theoretical and applied forestry. Further research in this field is therefore strongly encouraged.

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NET RETRIEVAL SEED COLLECTION

James L. McConnell and Jerry L. Edwards

ABSTRACT: The Net Retrieval Seed Collection System is a mechanical seed harvesting system. It has been used successfully in southeastern seed orchards for the past several years. Techniques, machinery, and costs for the system are described.

INTRODUCTION

There are well over 6,000 acres (2 428 ha) of loblolly (Pinus taeda), 600 acres (243 ha) of shortleaf (P. echinata) and 300 acres (121 ha) of Virginia pine in the Southeastern United States. These species are all commercially important, with the loblolly pine far and away the most important. Also the seed is considered to be hard to collect because the cone is not easily freed from the limb. Traditionally, collecting cones has been the primary means of collecting seed.

With such large areas of seed orchards to collect during the short period between cone ripening and seed fall, seed orchard managers have sought a better method of collecting the high-value pine seed needed to reforest the southern pine wood basket.

The netting-seed collection concept, which originated with the Georgia Forestry Commission, shows promise as a method to collect seed. The Commission spread net material over the seed orchard floor and waited for the cones to ripen and the seed to fall. A hand labor force was used to windrow the material that had accumulated on the net. The windrowed material was hand-fed through a peanut harvester. The peanut harvester did a good job of separating the seed from the pine straw and other trash. Six years ago the USDA Forest Service's Southern Region and Missoula Equipment Development Center began development of a system that would mechanize the concept developed by the Georgia Forestry Commission. The initial goals were to provide a system that could be operated by five to seven people, harvest the seed in a relatively short period of time, and do all this in a safe manner.

The initial goals have been met. One net retrieval machine can safely harvest seed from 40-60 acres (16-24 ha), using only five to six persons and do the entire job. Elimination of the need for tree climbing creates a safer, more productive, and less labor-intensive method of seed collection (fig. 1). Except for poor seed years, the system has proven to be cost-effective. The seed orchard managers are extremely pleased. The system is presently on-line at three Southern Region orchards with the fourth scheduled this year. Several State and industrial orchard have begun the use of parts of the system.

Figure 1.--Netting retrieval and seed separation equipment.

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the net used in the system is a polypropylene plastic fabric manufactured initially as a backing for carpets. Knitted monofilament polyethylene fabric designed as shadecloth has also been used successfully (fig. 2).

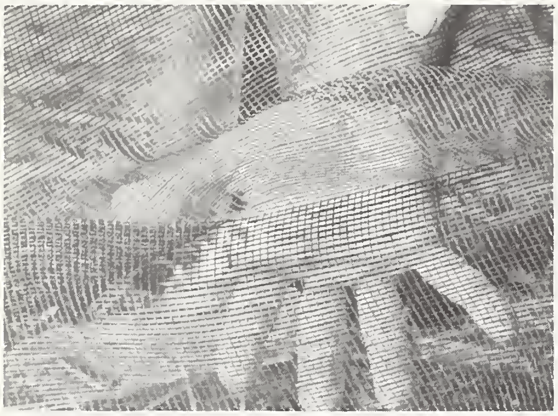

Figure 2.--Net (polypropylene plastic).

Optimum seed fall in the South usually occurs in November, but as with most outdoor activities, it depends on the weather. As weather fronts move through, rain occurs; after the front passes, several cool, dry, sunny days occur bringing good collecting conditions. The netting is spread over the orchard floor several weeks before cone opening (fig. 3).

Figure 3.--Orchard floor covered with netting.

As the cones open, orchard trees are shaken with mechanical tree shakers similar to those used to shake pecan trees. The specially designed cushioned clamping pads, when attached to the tree, tend to protect the tree and, at the same time, transmit the shaking energy to the tree. The omni-direction shaking characteristics developed by the shaker head removed nearly all the seed from the open cones. Experience has taught us that minimizing tree damage depends on a competent, well-trained tree shaker operator. A second shaking prior to retrieval yields additional seed from the cones. When the seeds have been dislodged from the cones and have fallen into the net, one end of the net is attached to aluminum pipe core which has been secured to the net retrieval machine. The retrieval machine operates by turning the core and rolling the net onto the core. Seed, pine straw, and other debris on the netting is dumped onto the retriever conveyor as the net is recovered and fed into the seed separator. The seed separator separates the seed from unwanted material (pinestraw, cones, sticks, etc.). The large amount of relatively clean pine straw processed can be bailed and used as mulch in nurseries or sold for landscaping.

The seed, as it comes out of the seed separator, is only roughly cleaned and requires additional cleaning and processing before being placed in cold storage. The seed receives additional processing at a conventional seed extraction facility. The seed requires fine cleaning and is introduced into the conventional processing equipment just after the cone tumbler and goes through the remainder of the seed cleaning/processing equipment. There is a substantial savings in cost since the expensive cone drying-opening process is eliminated.

EQUIPMENT

Power requirements to operate the netting retrieval and seed separation equipment are less than 30 PTO horsepower (34.4 kilowatts). The PTO power is used to drive a hydraulic pump that supplies the power to operate the machinery.

An operator's station is located at the rear of the retrieval equipment. From this location, all machine functions can be observed and controlled.

COLLECTION COSTS

In 1983, the net collection process produced 1,649 lb (748 kg) of loblolly pine seeds from 141 acres (57 ha) at three Southern Region seed orchards. Overall, 1983 was not a good seed collection year; total production and yield were down. The seeds were collected at the following orchards: Francis Marion, South Carolina; Erambert, Mississippi; and Stuart, Louisiana,

Variable Costs.--Labor and general-type equipment (vehicles, wheel tractors, etc.) costs totaled $29,920.

Fixed Annual Costs.--Fixed costs for 1983 were:

Item	Total cost	Expected life	Annual amortization
Netting	$316,214	10 years	$31,621
Cores	14,040	20 years	702
Retrieval Equipment	144,480	20 years	7,224
		Total	$39,547

Cost of net collection, 1983.--Total costs of net collection for the year were:

Category	Total Cost	$/acre	$/ha
Variable cost	$29,920	$212[1]	524
Fixed cost	39,547	280	692
Total	$69,467	$492	$1216

[1]Number of acres = 141 (57 ha)

1983 COLLECTION

Cones collected in 1983 from the same orchards yielded 1.14 pounds of seeds per bushel (0.12 kg/dl). The seeds collected from the netting system weighed 1,649 lb (748 kg). The equivalent number of bushels of cones required to yield the seeds obtained from the netting is 1,446 bushels (5 096 dl). The collection of cones obtained by contract or force account (using Forest Service workers) would have been $33 per bushel ($9.35 per dl):

Collection	$30
Drying and extraction	2
Transportation to extractory	1
	$33/bushel
($9.35/dl)	

The cost of cone collection FY 1983 (hypothetical) was $47,718 (volume of seed X cost/unit).

The comparison of costs (cone collection versus netting system) was:

$69,467	Cost of net collection
-47,718	Cost of cone collection
$21,749	

This proves that cone collection would have been more economical.

1984 COLLECTION

In Fiscal Year 1984, 4,529 lb (2 054 kg) of loblolly pine seeds were collected from 216 acres (87 ha) within the netting systems from the three Forest Service seed orchards mentioned earlier. Seed production was spotty; east coast collections were light, but Gulf coast collections were good to heavy.

Cost of net collection in 1984 was:

Category	Total cost	$/acre	($/ha)
Variable cost	$48,575	$225[1]	$ 558
Fixed costs	39,547	183	454
Total	$88,122	$408	$1012

[1]No. of acres = 216

The cost of cone collection in 1984 (hypothetical) was $104,511 (volume of seed X cost/unit).

The comparison of cost (cone collection versus netting system) was:

$104,511	cost of cone collection
- 88,122	cost of net collection
$ 16,389	

This proves that net collection would have been more economical.

RESULTS AND DISCUSSION

The cost of the net seed collection system is greatly affected by the volume of seed available. The larger the volume of seed on the net, the lower the cost per pound (kg) of the seed. Retrieval and quality of separation of the seed is virtually unaffected by the volume of seed. On the other hand, the volume of debris (pine straw, twigs, etc.) on the net has a measurable effect on the rate of separation.

In general, the smaller the seed and cone crop, the more the advantages are in favor of cone collections. When the crop is small, the cones can be selectively collected; however, it is nearly impossible to selectively deploy netting and still catch the seed fall.

The equipment now used for the net retrieval system is considered a first-generation production prototype. Many improvements will be made to produce a more efficient and compact system. The cost of equipment may continue to rise, but probably not as fast as the cost of labor, especially the trained labor force that is required in cone collection.

The initial costs of the net retrieval system are high. Therefore this system would not be economical in young orchards or an orchard with a low production capacity. The following factors can be used to decide whether to use the net system or harvest cones in a particular year:

Net Seed Collection System

1. Number of acres (ha) of orchard under consideration.
2. Calculated production capacity of the orchard (number of bushels (dl) of cones or pounds (kg) of seed in the orchard under consideration); end product will be pounds (kg) of collectible seeds.
3. Cost of deploying and recovering the net seed collection system on the following basis: a five-person crew operates at the rate of 0.25 acres (0.11 ha) per crew per day. This work includes the total job of deploying the net, shaking the trees (twice), retrieving the net, processing the seed, and returning the rolls of net to storage. The time sequence becomes relatively unimportant, because much of the job takes place before and after the cone ripening period. With this information, the orchard manager can calculate the price of seeds per pound.

Cone Collection System

1. Price per bushel (dl) to collect cones, transport them and extract the processed seed.
2. Can the cone crop be picked before cones mature to the point of opening?
3. Is an adequate supply of collection equipment available?
4. Is there an adequate pool of people to do the work safely?

If the price per bushel (dl) for the netting system is higher than that for harvesting cones, the orchard manager would then decide that, in all probability, cone picking will be the most economical method.

Every orchard and organization will generate a different number, but we feel the net retrieval seed collection system is a viable alternative to a difficult job. Netting material and tubing specifications are shown in the appendix.

APPENDIX

Netting material specifications

Material: Polypropylene/polyethylene plastic
Width: 16 ft, 5 inches (4.75 m)
Length: 350 ft (106.16 m)[1]

Salient characteristics:

Color	- Black
Weave count	- 6 X 8 per in^2
Weight	- Minimum 2.1 oz per yd^2 (50 g per m^2) Maximum 3.0 oz per yd^2 (17.4 g per m^2)
Tensile strength	- Minimum 60 lb warp (27 kg) warp (length) Minimum 70 lb (31.5 kg) fill (width)
Burst strength	- Minimum 175 lb per in^2 (12.2 kg per cm^2)
Yarn stability	- Minimum 1 oz (250 g)
Cores	- All cores to be continuous in lengths 17.25 ft (5.23 m) overall
Outdoors wearing	- Minimum of 70 percent retention after 400 hr in weather-o-meter.
Selvedge edge	- Minimum of 0.25 inch (0.64 cm) selvedge area for each edge.
Cost	- \$1.62/lineal yd (\$1.47/lineal m) @16'5" (4.75 m) width \$1418/acre (\$3545/ha) --1982 contract price

Source of supply:

Amoco Fabrics Company
Patchogue Plymouth Division
550 Interstate North Parkway
Atlanta, GA 30339
(404) 995-0935

Weathashade
568 West Orange Blossom Tr.
Apopka, FL 32703
(305) 889-3692

[1]Length can be varied to meet needs of the individual orchard.

Core (tubing)

Material:	Aluminum Alloy 6063 T6
Diameter:	4.0 inches (10.6 cm) outside diameter
Length:	17 feet, 3 inches (5.23 m)
Weight:	0.73 lb per lineal foot (56.5 g per lineal m)
Specification:	Federal Specification QQ-A-200/9c
Cost:	\$20/piece (approximate) --1982 contract price

Source of supply:

Reynolds Metals
6601 Broad Street
Richmond, VA 23261
USA (804) 281-2655

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DOUGLAS-FIR SEED COLLECTION AND HANDLING

Richard M. Schaefer III and Daniel L. Miller

ABSTRACT: High-quality conifer seed is a must for successful and economical seedling production, especially in containerized operations. High-quality seed is characterized by high percent germination (90+), uniform germination and insignificant mold and disease problems. High-quality seed can be assured by attention to details during collection, handling, and processing. Collections should be made only after the seed has fully matured. Immature collections result in reduced and erratic seed germination. Proper cone handling and storage methods will prevent problems associated with cone heating and molding. Skillful processing will produce clean, dry seed and will preserve the germination potential obtained through proper collection and handling.

INTRODUCTION

Seed collections must stress quality as well as quantity. Seed quality is especially important in greenhouse nurseries. As containerized seedling production increases so does the need for high-quality seed. For instance, using a seed cost of $5.00/M seedlings, increasing germination from 50 to 95 percent increases seed value by five times (table 1). Actual growing costs associated with the lower germination potential seed are considerably higher than the single-sown 95+ percent germination seed because the increased seed volume means higher stratification, sowing, and crop thinning costs. Additional savings for 95+ percent seed could be as much as $5-$10/M in container nurseries. The 95+ percent germination seed also reduces grower risk from additional failures caused by fungus and low-vigor seedlings resulting from poor quality seed.

Table 1.--Douglas-fir seed values per pound for a containerized nursery assuming a $5.00/M seedling seed cost

Germination Percent	Seeds per Cavity[1]	Seeds Per Pound 25M	35M	45M
95+	1	$125	175	225
75	3	42	58	75
50	5	25	35	45

[1]Assumes a sowing rate that will produce at least 95 percent stocked containers.

Paper presented at the Conifer Tree Seed in the Inland Mountain West Symposium, Missoula, MT, August 5-6, 1985.

Richard M. Schaefer III is Seedling Production Supervisor, and Daniel L. Miller is District Forester, Potlatch Corporation, Lewiston, ID.

High-quality seed also reduces seed inventory and storage costs. Prior to implementing the procedures described here, our Douglas-fir seed germination rates ranged from 12 to 39 percent. Assuming this seed is usable in our nursery, we would need an additional $675,000 in seed inventory to operate at current capacity. High-quality seed is also important in bare root nurseries, especially as precision seeders come into use.

These dollar values become more important when you consider that obtaining high-germination seed costs no more than obtaining low-germination seed. The secret to high-quality seed is attention to detail. Cones must be harvested when seed is ripe and handled and stored so as to preserve seed quality. It costs just as much to harvest immature seed with 30 percent germination as it does to collect mature seed with 90 to 100 percent germination. In fact, immature or insect damaged seed is often more difficult to extract. This increases processing costs and reduces seed yields.

The methods described here were developed from communications with the late Mr. Charles Brown of Brown Seed Company, Vancouver, Washington. Charlie's methods were developed during more than 30 years of working with conifer seed. His goal was to produce the best possible conifer seed. To do this, he found that the cones must be fully ripe when collected and stored under proper conditions. If not, seed viability was reduced. His cone maturity indicators are the result of years spent observing cone ripening. These cone handling procedures were developed to prevent molding which reduces seed germination and avoid cone heating which causes varying dormancy levels. Under Charlie Brown's direction, Brown seed earned the worldwide reputation of being the best available. This is ample testimony that his procedures work.

The following are Brown's methods that Potlatch foresters are using. These methods have resulted in the collection of consistently high-quality Douglas-fir seed with germination rates of 85 to 99 percent.

SEED INVENTORY PLANNING

Douglas-fir usually produces a medium to heavy cone crop once every five to seven years in northern Idaho. At Potlatch, we strive to maintain a five-year seed supply on hand for each seed zone. We have delineated seed transfer zones by ± 500-foot elevation classes and by 15-mile geographic distance within the same habitat type. Five-year harvest plans are used to estimate the number of seedlings and amount of seed needed for each zone. Collections are scheduled only during heavy cone crop years

unless seed inventory is low for specific zones. Estimated seedling needs are converted to pounds of seed and bushels of cones for planning and budgeting purposes. These estimates are developed during the winter so that selected areas can be checked for potential cone crops in early spring. This planning also allows scheduling logging to prevent harvest in selected collection areas prior to cone ripening. This is especially necessary for fall-and-pick cone collections, our preferred method. Also, other stands may be reserved as permanent cone collection areas. This is especially important if there are few trees of the desired species of cone bearing age within the seed zone.

EARLY CROP ANALYSIS

Potential cone crops can be evaluated as early as mid-June. By then, the female cones have been pollinated and are large enough to be easily seen. Also, cones damaged by spring frosts can be easily identified. These turn red-brown and shrivel. Cone crops can be rated as follows:

Light crop - few scattered cones, usually near tree top and limb ends.

Medium crop - several cones per limb, majority in the upper 1/3 of crown.

Heavy crop - 10-20 cones per limb and extending down most of the crown.

For a crop to be rated heavy, most of the trees in the stand should have heavy crops. Scattered trees with heavy cone crops don't necessarily indicate a good collection year. Unless seed is badly needed, collections should not be scheduled in light to medium crop years. Seed yield is generally poor in light to medium crop years because of poor pollination and increased insect damage. Seed and cone insects may destroy nearly all seed during light crop years. Since it costs as much to collect wormy cones as good ones, collections should be scheduled when you can get the most seed for your efforts. An elementary but important fact to remember is that collection costs and extraction costs are rather fixed; the amount and quality of seed recovered is the major variable. So unless seed inventories are critically low, only moderate to heavy crops should be collected to avoid higher costs and lower percent germination lots.

Seed count monitoring should begin in mid-July. By then, seeds have developed far enough to produce accurate counts. Cones may be picked or shot down for inspection. Check cones for insect activity. Mid (July) season insect attack shows as curled, brown tipped or dead, dry cones. Insect bore holes and frass may also be evident. Insect damage may not be easily noticed, however, so cut tests should be a standard part of crop evaluation procedures. The cut test is made by slicing cones longitudinally down the center with a <u>sharp</u> knife, hatchet or cone cutter.

Tests are conducted as follows:

- Sample at least 10 cones from each of 4 to 5 trees selected at random in the stand.
- Count all sound filled seed on one face of the cut cone. Filled seed have white centers (endosperms). Aborted seed are darkened or shriveled. Look for insect activity inside the seed.
- If more than half of the cones sampled have insect damage, subtract one sound cut seed from the count on each damaged cone. Insect-damaged cones often do not fully open during processing, preventing extraction of all sound seed. Adjusting the seed count compensates for this.
- The number of filled seeds should average at least 5 for economic harvest. Lower counts can be accepted depending on the need for the particular source.
- A 6 or better count is considered adequate for a large collection effort.

Samples should be collected on at least two-week intervals to monitor maturity and insect damage. Insect damage will increase as the summer progresses. Some crops that appear good in July may be completely destroyed by harvest time.

COLLECTION PLANNING AND PREPARATION

Planning cone collection activities involves determining the type of collection. Preparation involves obtaining needed equipment and preparing storage facilities. The type of cone collection -- climb and pick, fall trees and pick, or squirrel cache -- will have an effect on seed quality. Unless absolutely necessary, squirrel cache collections are avoided because it is impossible to consistently get 90+ percent germination from squirrel-cut cones. This is due to two factors:

1. Squirrel cache collections are characterized by inconsistent maturity levels and large variations in dormancy, resulting in lower and extended germination. The squirrels do not always wait until seeds are fully mature before cutting cones.

2. Squirrel cache collections have the high probability that cones and resulting seed will be <u>highly</u> contaminated with various disease-causing fungi. This is due to the cool, moist environment in the cache. Tests run at the Potlatch greenhouse facility have shown up to 14 times more germinate mortality in Douglas-fir squirrel cache seed lots than in hand-picked seed lots.

In many of the squirrel cache lots, correlation between germination tests and greenhouse performance is very poor. Hand-picked cones, on the other hand, usually have operational performance similar to that of current germination tests.

Preparation is one of the most important steps following confirmation of the collectible cone crop. This involves:

1. Having adequate field personnel to handle cone maturity checks and clean, bushel, and tag cones.

2. Providing a secure area adequate for daily cone storage.

3. Having enough clean 1.5-2 bushel burlap collection bags. Dirty or previously used bags may reduce quality enough to lower the percentage of the germination testing.

4. Determining numbers, volumes, and species to be collected in each area.

5. Giving proper notification to the required number of cone pickers to handle the harvest. This would include the type of harvest, prices paid to collect, cut test specifications, acceptable maturity, etc.

6. Obtaining adequate field storage racks and developing cone transportation plans. Long-term storage requires a covered area to protect cones from rain and rodents that allows adequate air flow for drying.

CONE MATURITY MONITORING

Cone maturity monitoring is a prerequisite for scheduling collections. Maximum seed germination is possible only when cones are harvested when the seed is fully ripe. Early harvests reduce germination. Immature seed are more difficult to extract, have lower germination and highly variable dormancy and may lose viability in storage sooner than mature seed. If in doubt, wait. It is wiser to lose some seed due to cone opening than to waste time and dollars processing immature seed. Cone and seed characteristics provide our most reliable maturity indicators. Year-to-year fluctuations in weather patterns affect cone ripening and make it impossible to set calendar dates for harvest. Elevation also affects maturity dates. Therefore, on-site cone inspections at each collection point provide the most reliable information for scheduling cone harvest. Remember, a sound regeneration system is based on mature, high-quality seed.

Cones should be checked at least every two weeks during July and early August. These checks will identify insect losses. Weekly or twice weekly checks should be made as cones mature. Cone color is not the best indicator of seed maturity. Examine the seed. Often it will mature before cone color changes. Mature seed endosperm is quite firm, nut-like and not milky or runny. Squirrel activity should not be used as a basis for starting collection activities. Squirrels are interested in food, not 90+ percent germination seed. A good example of the squirrel's inability to evaluate seed maturity occurred in 1980. Several seed companies collected *Abies grandis* cones in north Idaho from squirrel cache sources. The seed extracted from several hundred bushels had such low germination percentages that the seed was not marketable. This could have easily been avoided by people trained to personally evaluate cone maturity.

The following Douglas-fir seed and cone maturity descriptions were developed by Charlie Brown and have been used successfully by Potlatch foresters since 1977.

Seed

Immature seed are white to cream-colored with clear to white wings. As the seed matures, the seed coat turns tan then dark tan as the wing turns brown. Mature seed has a golden brown seed coat with completely brown wing.

Cones

Immature cones are green. As they ripen, they acquire a yellow tinge like a ripening banana--not bright yellow but slightly yellowish. As they lose their yellow tinge and begin turning brown, they puff up. Bracts turn brown first and are the first indicator of approaching maturity.

Seed is ripe when cones puff. This is weather related. High humidity will keep ripe cones tight. Cones won't drop seed until they turn brown and open.

Cutting mature cones logitudinally through the center will reveal brown lines (seed wings) running from the seed to the scale tip. If the brown wing isn't obvious, the cone isn't mature. The cut surface of immature cones will turn brown (like a cut green apple) within five minutes. Near ripe cones will too, but not as rapidly.

CONE HANDLING AND STORAGE

The following guidelines will ensure quality seed from the cone receiving station to the processor:

1. Cone pickers are required to turn in harvested cones daily. Filled sacks should be kept in the shade during the day and not stacked together, especially not in car trunks. Cone heating must be prevented.

2. All cones are run over a cleaning table to remove debris, check maturity, perform cut test counts, measure for payment, and label. Bags are double tagged--one inside the bag and one tied on the closure (figure 1).

3. A maximum of one bushel of cleaned cones is placed into 1.5-2 bushel sized loose-knit burlap bags. This allows room for air circulation as cones expand and open. The bag is placed as quickly as possible on a portable field drying rack. Quite often, short distance transport of cones to a more central area is required. Since fresh-picked cones are quite susceptible to heating, arrangements must be made to have the green cones shipped immediately, unloaded, and re-racked before heating damage occurs. Green cones will heat, just like piles of wet hay or

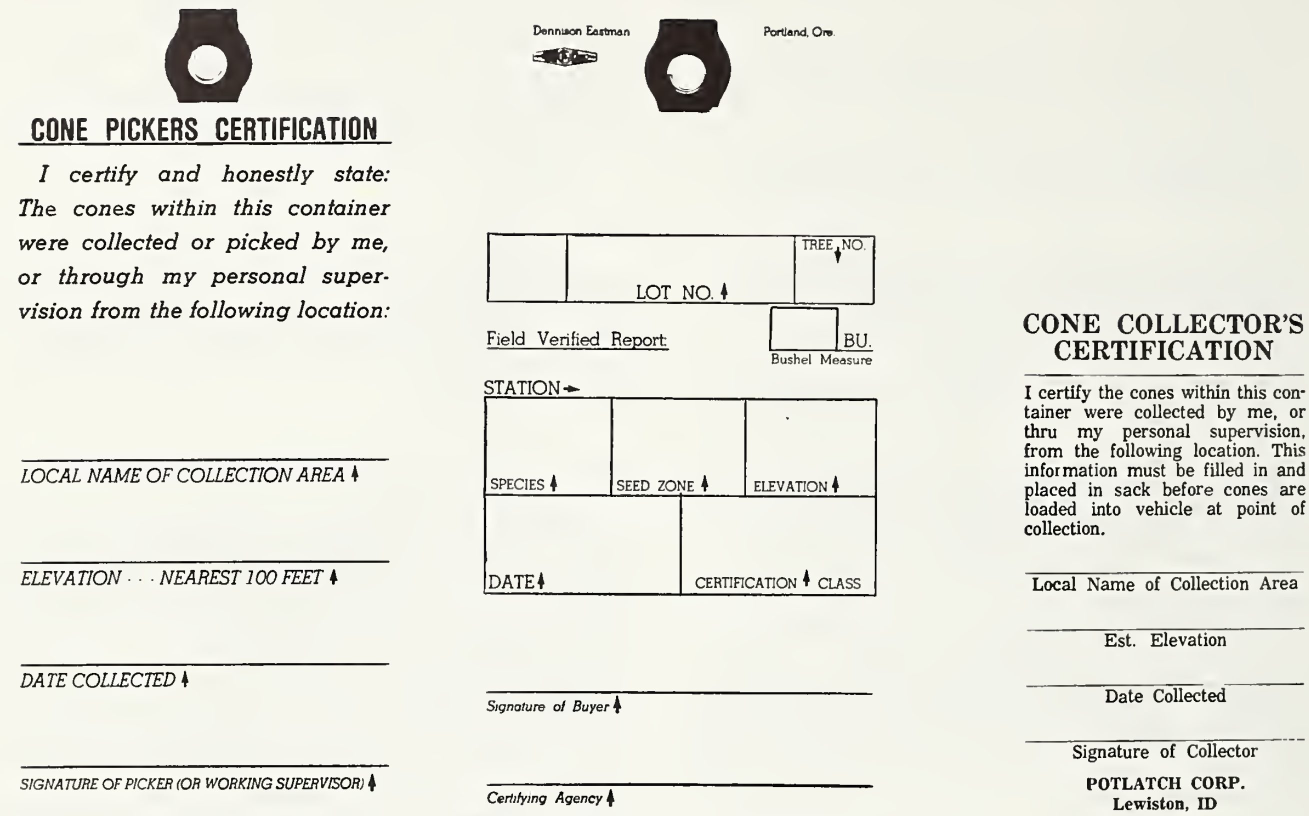

Figure 1.--Cone bag tags used successfully in Potlatch operations.

grass. Green cones can be stacked together for 1-4 hours; you can test for heating by putting your hands between the piled sacks. Cone heating can reduce dormancy homogeneity that affects stratification time and produces mold problems.

4. To promote seed lot homogeneity, the fresh field-racked cones should be allowed to "after-ripen." This simply means the cones should be kept for approximately a two-week period in a dry, shady, well-ventilated, cool area. This allows the cones to slowly begin drying. During this period, the seeds in each cone have time to reach almost equal dormancy levels; if done properly, this can apply to the entire seed lot. After proper stratification, the result will be quick, uniform seed germination.

5. Following after-ripening, cones may be air-dried before shipment to the processor. If early shipment for long distances is required, precautions are needed to avoid cone heating. Potlatch Corporation has found, in our northern Idaho climate, that two months of air drying brings the seed moisture levels down to approximately 15-20 percent. At this level, there is no trouble with cone heating if the bags are tightly stacked for 24 hours. Each person responsible for collections will have to determine how best to avoid cone heating.

The final link in the process of obtaining high-quality seed is the extracting and processing facility. Improper cone and seed processing can negate all the care taken in the collection process. Only processors with a good reputation for producing clean, high-quality seed should be used. If possible, visit the facility and observe their procedures. High-quality seed is clean. It does not contain pitch nodules or other inert debris. It also does not contain damaged seed. Blank seed should be removed during cleaning and proper processing will not produce cracked or damaged seed. Properly handled and processed seed should smell good, not sour.

TEAMWORK NEEDED

To produce high-quality seed, all steps from inventory planning through collection and cone storage must be done correctly. Improper methods applied anywhere in the process can substantially reduce both seed yield and germination. Since vigorous, high-quality seed is necessary to produce seedlings that meet rigid specifications, both field personnel responsible for seed procurement and nursery managers must work together to assure that proper seed collection procedures are adhered to.

AERIAL CONE HARVESTING IN BRITISH COLUMBIA

D.P. Wallinger

ABSTRACT: Early attempts to devise an efficient means of harvesting cones with the use of a helicopter were not totally successful but the results were promising enough to encourage continuing development. At present, two methods--raking and clipping--meet air transport and safety guidelines, and are in common use.

In raking, a basket-like device is lowered over the upper tree crown and the cone-bearing branches are stripped from the stem as the unit is raised by the vertical lift of the helicopter. In clipping, the helicopter hovers at the upper tree crown while an operator, using a hydraulic pruner or electric chainsaw, cuts and recovers the cone-bearing top or branches.

Each of the methods has specific applications and limitations regarding stand type, species, and weather. Operating procedures and training requirements for clipping have been identified and documented. Productivity of aerial cone harvesting has been shown to be competitive with traditional collection methods and a significant volume of cones is now collected aerially in British Columbia.

BACKGROUND

The harvesting of cones by aerial means had probably been on quite a few minds for quite a few years, but it wasn't until the mid-1970's that somebody did something about it.

Our first knowledge of an aerial system was the scion collecting device conceived by Pete Theissen of Pacific Northwest Region, U.S. Forest Service, in 1974. This system has come to be known as aerial clipping and will be discussed in more detail later. It is also the standard method of scion collecting in British Columbia today.

In 1974, Okanagan Helicopters, with Forest Service input, fabricated a suspended, unmanned device for collecting scion material. However,the "Cage" suffered from cold weather stress and was scrapped.

In 1976, two forest companies adapted the clipping system for operational collection of Abies amabilis fir. In one case, the cone-bearing branches were clipped and stowed in the poly-lined passenger compartment. On the other project, an operator hooked a small choker on the stem and cut off the top with a small chainsaw. The recovered top was suspended from the cargo hook as other trees were harvested.

Concurrent with these developments, Jack Walters at the University of British Columbia Research Forest had designed an aerial cone rake. Jack's unit was developed under a service contract with the Canadian Forestry Service and was operationally tested in fall 1976. True to Jack's philosophy of "think big," the rake was enormous. It stood 7 m (23 ft) high, was 4.5 m (15 ft) in diameter at the base, and weighed over 800 kg (1800 lb). While the unit's performance was not favorable on a cost-benefit basis, Jack's creation provided the spark that was needed to get things "off the ground."

In the next year or two, the sky was filled with all kinds of raking hardware--kind of like a forestry space program. Most of this metal joined the "Cage" on the scrap heap. Two commercial developers did design successful rakes, but only one has survived.

In the meantime, aerial clipping on a production scale was becoming reasonably successful. Equipment was more sophisticated and procedures refined. An electric chainsaw was introduced as an option to the hydraulic pruner.

The "flying gondola" was conceived aft r a monsoon bucket had been used for samp ng during the spruce budworm outbreak of 1975-1976. First thought of as a means of scion collecting, the gondola quickly became a vehicle for cone harvesting. The bucket was slung beneath a Long Ranger and maneuvered into the treetop. The saw operator, riding in the bucket, set a small choker around the stem and sawed off the top. The severed top hung from the bucket while subsequent trees were harvested. This was a highly productive system

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and two or three units were built and used in 1979. Unfortunately, because a single-engined helicopter was used, the method was grounded by the Federal Ministry of Transport. Its use would likely be permitted if two-engined aircraft were used but the economics of the method would be unfavorable.

So that leaves us, at present, with two approved aerial harvesting systems--raking and clipping.

RAKING

The term "rake" loosely refers to branch collectors, strippers, or cutters. The configuration is generally a circular or hexagonal fiberglass cone at the top of which is a large opening with wide, radiating slots, each of which is bordered by upward-oriented cutting edges. Around the circumference of the base is a vertical fence of expanded aluminum welded to a frame. The diameter of the rake is normally about 2 m (6.6 ft). From three points around the circumference of the upper frame, light cables rise to a common ring to which the helicopter's cargo hook is attached. The unit may weigh between 130 and 150 kg (285-330 lb).

In practice, the rake is centered over the target tree and lowered until most of the cone-bearing branches protrude through the upper opening of the rake. The helicopter then lifts the rake and the cutting edges sever the limbs which are then retained by the surrounding mesh. Two or more lowering and lifting sequences may be required to harvest the majority of available cones from a tree. Harvesting takes about 30 seconds per tree. The pilot then proceeds to other trees and repeats the procedure until he has a safe maximum payload.

At the landing, while the helicopter hovers, the dumping mechanism is activated by the ground crew and the collected material falls free of the mesh enclosure. Any pieces hung up in the rake teeth are cleared by hand. The dumping device is then secured and the machine leaves for another cycle. A cycle is defined by a series of harvesting events--lift-off, fly-out, harvest, fly-in and unload. Cycles are usually under 15 minutes during which time eight to twelve trees may be harvested. Pilot fatigue is a safety consideration and two pilots usually alternate the flying task every hour or so. A day's collecting lasts about 7 1/2 hours or 3 1/2 hours per pilot.

The Bell 206L-1 (Long Ranger) or Hughes 500 are adequate machines for raking. In 1979, it was determined that, to be successful, aerial rakes must be:

a) simple in design and easily maintained;
b) light in weight but strong;
c) suitable for several species and capable of harvesting several trees in one flight;
d) stable in flight and easily maneuvered; and
e) efficiently unloaded.

The rakes in use today meet these criteria and they are very efficient for harvesting the species for which we have a large demand, namely true firs, spruces, and Douglas-fir.

Rakes can be used in all types of terrain. They can be ferried short distances between collection areas or can be transported over longer distances by pickup truck. New unloading mechanisms enable harvested material to be dumped into the box of a large truck and hauled to a central picking facility.

With improvements in rake design and experience, productivity has become quite favorable. In fact, collecting true firs by conventional methods could never match the productivity of the rake.

The only drawback to raking is that the selection of phenotypes is left up to the pilot. In our situation, where considerable emphasis is placed on collecting only from better phenotypes, we are dependent on carrier-employed pilots. They are usually anxious to maximize productivity, and we all know that the most cones are not always on the best trees.

Another concern with raking is cone recovery. Our best estimate is that only about 50 percent of the cones on a tree are recovered. As long as there are lots of trees available, this is not a problem, but when a quota must be taken from a stand with a limited number of cone-bearers, cone recovery is important.

CLIPPING

The development of clipping to its present state has been a cooperative effort between the Ministry of Forests and the carriers who have done the flying for us.

The system involves some modifications to the aircraft itself. It must have:

a) low skid gear - no bear paws;
b) front and rear doors on the right side removed;
c) live-mike capability between pilot and clipper operator;
d) a barrier between the rear and forward cabin areas;
e) the rear cabin lined with poly;
f) an E.L.T. (Electronic Locator Transmitter);
g) a hanger for the clipper installed by the right hand step; and
h) a counter-balancing weight secured in the left side of the forward cabin to maintain center of gravity.

Following several incidents in 1982, the Ministry of Forests set up a committee to review the aerial clipping system and to establish operating procedures. In cooperation

with the air carriers, an operations manual and a formal training program were produced by the Ministry and are now in place. Because clipping demands precise flying, pilot requirements and qualifications are stringent. Clipper operators must undergo an intensive "hands-on" training course. The pilot and operator must work as a team, so their personalities must be compatible.

Briefly, the clipping unit has three components. The auxiliary power unit consists of a battery pack and is independent of the helicopter's electrical system. However, the battery pack can be replaced by connecting the hydraulic pump unit directly into ship's power.

The hydraulic pump consists of an electrically driven hydraulic unit, a hydraulic reservoir, and switching valves. The electrical circuit can be activated by a master switch.

The third component consists of the hydraulically operated clipper head, hydraulic hoses, and an electrical cable which leads to an operating switch on the handle of the clipper. The clipper must cut through a 6-cm (2 1/2-inch) stem in three seconds.

The electric chainsaw option is made up of two components. A generator is mounted to the left front floor of the aircraft and is wired to the aircraft's electrical system and produces 110 volts to power the chainsaw. The electric chainsaw is equipped with a short bar and a special guard which covers the entire chain except for a 6-cm (2 1/2-inch) opening along the underside of the guidebar.The operator wears natural-fiber coveralls, appropriate footwear, suitable gloves, and a secured and visored helmet fitted with voice-operated headset. In the clipping position, the operator is seated on the step of the right rear door with his feet on the skid. He is secured to the aircraft by a special body harness attached to an interior hard point and also by the regular seat belt extended by a lanyard.

Prior to each day's operation, there is a briefing session and inspection of equipment. During the day, whenever the aircraft is refuelled or shut down, there is a routine 14-point check of the helicopter, equipment, and safety gear. The daily routine also includes a full debriefing at which discussion is recorded and is often very candid, to say the least. These sessions are valuable for pointing out potential hazards or improving technique.

In flight, the clipper operator is responsible for tree selection but the pilot has the final say on the basis of safety. When agreement on a tree is reached, the pilot checks local winds and moves the aircraft into position while the operator checks the area around the tree for any hazards and advises on tail rotor clearance. As the machine is brought up to the tree, the operator checks his harness and readies the clipper. When the skid touches the tree stem, the cut is made and top recovered. As the pilot pulls away, the top is stowed in the rear cabin. This is all done in a series of smooth actions with constant communication between pilot and operator. Ten to twelve tops may be clipped during an 8-10 minute cycle. The "what ifs" associated with in-flight clipper problems, loss of communication, injury, or helicopter malfunction are a part of the daily briefing. Anything which occurs that disrupts the smoothness of the operation is considered to be an incident and is discussed at the debriefing.

Aerial clipping is both physically and mentally demanding, so that rest periods for both pilots and operators are rigidly enforced and daily flying times, using two air crews, are the same as for raking. Normally, the Bell 206B (Jet Ranger) is used on the clipping operation.

Clipping is suited to harvesting where the cones are concentrated in the top of the crown. Spruce, especially, is conducive to clipping because practically all the cones are located in the top 3 m (10 ft) of the narrow conical crown. The method is also used effectively on immature Douglas-fir, but when more than one approach to the same tree is necessary, as for true firs or white pine, efficiency declines.

Providing the clipper operator is an agency employee, clipping affords the best opportunity for tree selection on the basis of phenotype, cone ripeness, and the incidence of insect-infested cones. The quality of cones harvested is, therefore, as good or better than when trees are felled or climbed. However, there are disadvantages. The method is not too safe in steep terrain, especially if there is a high frequency of snags. The size of tops which can be harvested is limited to about 2.4 m (8 ft) and to a stem diameter which the clipper will accommodate. Because of rotor wash, holding hover while at the tree is often difficult. The cost of fabricating and installing the clipper unit, preparing the helicopter, and training and outfitting operators is considerable. However, much of this cost is a one-time investment.

AERIAL SYSTEMS IN GENERAL

The use of helicopters provides a little excitement into an activity which, we all know, is far from glamorous. Consequently, we are finding that there is a tendency for the aerial systems to be prescribed for situations where they are not always warranted. People seem to think that aerial systems are the panacea which will end all their problems. This is not so; the criteria for success are demanding.

A collection is measured by the amount of clean seed it yields, so right off the top, high filled-seed counts are a must.

The economic success of the collection operation itself is predicated on maximizing the volume of cones delivered per flying hour. Therefore the crop must be heavy and the species suitable. Present aerial systems are marginal for the cedars and western hemlock and are definitely not suited to ponderosa and lodgepole pine or to western larch. Harvesting is from dominant and codominant trees which have narrow, conical crowns.

Stands should be even-aged and at the peak of their cone-producing years, and should be within about 4 km (2 1/2 miles) of road access or a log landing so that fly-in and fly-out times are short.

Aerial collections require good planning to acquire helicopters and equipment, schedule areas, and to coordinate operations so as to minimize ferry time. Pre-organization is based on a good knowledge of the stand and the surrounding area. This involves a reconnaissance flight to:

a) establish geographical and elevational boundaries;
b) confirm with the pilot the species and types of trees to be harvested;
c) select and check approaches to dump sites and fuelling areas;
d) note hazards to the flying operation such as snags, large birds, powerlines, and industrial or recreational activities; and to
e) develop a pattern for harvesting the stand.

The delivery of helicopter fuel is one item in particular that has to be checked; if the truck delivers to the wrong area, you have a costly problem.

Dump and pick sites must be separate from the fuelling area. They must be accessible, firm, and free of dust or debris. Helicopter approach and departure paths must be flat and clear of obstructions. A few simple wind-indicators (flagging tape) are desirable.

Pickers should not be allowed to work on a landing that helicopters are using. Therefore, several dump sites are advisable or the picking can await the completion of the aerial phase. The other option mentioned earlier is to haul the harvested material to a central facility where the pickers can enjoy shelter, and freedom from noise, dust, and bugs. This requires extra monitoring--one person checking seed set, ripeness, and insect damage at the

Table 1.--Percentage of cones harvested by aerial methods in British Columbia, 1979-83 (registered seedlots only)

Species	1979 Total (Hl)[1]	1979 % Aerial	1980 Total (Hl)	1980 % Aerial	1981 Total (Hl)	1981 % Aerial	1982 Total (Hl)	1982 % Aerial	1983 Total (Hl)	1983 % Aerial
True firs										
Alpine	22.0	-	7.8	-	-	-	18.0	-	-	-
Amabilis	1833.6	91.6	45.8	100.0	-	-	707.8	93.4	350.0	99.1
Grand	-	-	13.5	81.5	115.9	100.0	121.3	81.5	25.0	100.0
Douglas fir										
Coast	621.0	2.9	213.7	-	85.6	-	1431.3	46.1	276.6	-
Interior	311.6	-	822.6	-	-	-	1354.3	13.9	42.0	-
Spruces										
Sitka	1153.2	2.7	1.3	-	0.4	-	2.3	100.0	207.3	40.4
Interior	10074.4	8.7	302.4	13.6	-	-	2762.7	48.1	4308.4	89.2
Hemlocks										
Western	228.3	4.4	1.0	-	21.1	-	319.9	59.6	11.6	43.1
Mountain	83.4	14.3	-	-	-	-	52.2	38.5	5.2	80.8
Cedars										
W. red	93.5	-	13.6	-	3.3	-	73.7	19.0	52.6	-
Yellow	-	-	1.0	-	5.1	-	-	-	1.8	83.3
Pines										
Lodgepole	899.3	-	1356.8	-	587.9	-	148.9	-	1020.8	-
Ponderosa	4.0	-	11.8	-	-	-	-	-	50.6	-
W. white	17.5	-	19.6	-	74.0	6.8	32.5	25.2	4.8	100.0
Larch	-	-	195.7	-	-	-	32.5	-	20.8	-
Total/ Mean	15341.8	20.7	3006.6	3.2	893.3	14.0	7292.3	43.5	6377.5	67.7

[1] 1 Hl (Hectolitre) = 2.75 (Imp.) = 2.83 (U.S.) Bushels, approx.

dump site, while another monitors cone cleanliness at the picking site.

Aerial harvesting permits collections to be made from areas which are presently inaccessible but likely to be logged in the near future. This means that cones can be processed, seed cleaned, and the stock grown for the area by the time it is logged and prepared. Cone crops can also be harvested from desirable stands which have been reserved for streamside protection or game corridors. Damage to tree crowns and whether or not the mutilated tops become entry points for diseases or insects is also a consideration. Our philosophy is that in most cases, the trees from which cones have been harvested will themselves be harvested in the next few years. In addition, many trees suffer similar damage naturally from snow, ice or wind breakage, and insect populations. Where clipping is used, this consideration is at least minimized by having only one clean cut.

As with any air operation, good weather favors safety and efficiency. Helicopters working in a hover position are particularly sensitive to wind, and to rain when it affects visibility. On cone harvesting operations, winds must be steady and less than 32 km (20 miles) per hour; the ceiling must be at least 150 m (500 ft) above ground; horizontal visibility must be at least 0.8 km (one-half mile) and there must be no impairment due to rain on the bubble.

As mentioned earlier, safety is the controlling factor in any aerial method. We are well aware that if a tragedy occurs on any aerial harvesting operation, then all operations will likely be shut down--at least temporarily--by the federal Ministry of Transport or the Workers' Compensation Board--or both. We believe that this unfortunate situation can best be prevented by:

a) employing certified, capable, and well-trained practitioners;
b) maintaining established and documented procedures backed up by strict discipline;
c) using safe, efficient, and well-maintained equipment; and by
d) continually monitoring the program with debriefings and post-collection "beef" sessions.

EXTENT OF PROGRAM IN BRITISH COLUMBIA

Table 1 outlines the percentages of various species harvested aerially in B.C. during the past five crop years.

Aerial systems have had a high profile (over 90 percent) in the collection of true firs, and are increasing at a steady pace in the harvest of what we call interior spruce which is white, Engelmann, and their natural hybrids. In the last good crop year, over 3800 hectolitres (10,500 bushels) of interior spruce were collected aerially. The reforestation program in B.C. is expanding and will soon reach 200 million trees annually, so it looks like cone harvesting from natural stands will be around for a few years yet.

PRODUCTIVITY

I do not want to discuss dollar costs because they change every year and are meaningless unless the input factors and collection circumstances are similar. Besides, some of our costs would likely make you people south of the 49th parallel shake your heads. Remember, however, that in B.C. we are talking about hectolitres, which are about 2.8 times the U.S. bushel. We are also operating in an economy where we're paying the equivalent of $1.86 for the same gallon of gas that you pay $1.15 for. What we do know is that with aerial collections, there is considerable economy in scale, that is, large collections.

Table 2.--Proportional costs[1] of stand establishment estimated for 1983-84 (108 million seedlings)

Activity	$/1000 seedlings	@ 1150 Seedlings per Hectare[2] $/hectare	¢/seedling	% of total cost
Cone collection	3.00	3.45	0.3	0.5
Seed processing	0.42	0.48	0.04	0.1
Nursery	175.00	201.25	17.5	29.7
Site preparation	166.90	191.93	16.7	28.4
Planting	242.60	279.00	24.3	41.3
Total	587.92	676.11	58.8	100.0

[1]All species, all stock types, all methods; and including production overhead (excluding administration)
[2]Hectare = 2.47 acres (approx.)

Predictably, the costs of delivering the top material to the ground and the shucking and bagging of the cones account for 80-90 percent of the total collection cost. The relative proportion of these two major items appears to depend on cone size and, to some extent, on the size of the branch pieces delivered.

Shucking of true firs is least costly, with Douglas fir, spruce, hemlock and cedar following in that order. In general, clipped tops are easier to pick from because pickers handle only one piece and more cones are intact. Raked material is more fragmented and many smaller pieces must be sorted through.

Our philosophy concerning collection costs is that they are a very minor proportion of the total cost involved in stand establishment. Table 2 indicates that (in 1983-1984) cone collection costs represent about one-half of one percent of the total cost of our restocked hectare.

Actually, the proportion is a bit lower because the seed used has usually been collected and processed in an earlier year when costs would have been less. So we feel that what may seem to be a large increase in collection cost is really only a small increase in total cost of the planted tree. If aerial collection improves seed quality or yield, then we are actually money ahead. Cones from the topmost portion of the crown are likely to have a high seed-set, and the propensity for "selfing" is minimized.

Productivity is best measured by the volume of cones delivered per flying hour, and depends on three factors.

The first, cone volume delivered per cycle, is a function of the:

a) abundance of the crop, (the number of cones per tree and the frequency of cone-bearing trees);
b) the size of the cones;
c) the percentage of cones recovered;
d) the design and efficiency of the equipment;
e) the ability of the air crew; and
f) the size and maneuverability of the helicopter.

The second, elapsed time per cycle, depends largely on the fly-in and fly-out distance. Short cycle times reflect a sound reconnaissance, good pre-organization, and an efficient team operation.

The third factor, picker productivity, is influenced by the species (size) of the cones and the size of the material delivered. The pickers' diligence and attitude is important

Table 3.--Productivity of aerial harvesting (based on data acquired to 1984)

Species	Cone crop Level	Number of collections	Total cones collected (Hl)[1]	Productivity Hl/harvesting hour[2] Lowest	Highest	Average
			Aerial Raking			
Coast D-Fir	Med-Hvy.	3	81.2	-	-	4.3
True firs	Hvy.	13	1663.0	5.7	20.2	14.2
W. hemlock	Med-Hvy.	7	106.2	-	-	2.2
M. hemlock	Med-Hvy.	2	7.8	-	-	3.0
W.R. cedar	Med.	3	13.7	-	-	2.7
Interior spr.	Med.	3	473.2	1.3	2.7	2.6
" "	Hvy.	2	752.4	2.0	3.6	3.4
			Aerial Clipping			
Interior spr.	Med.	3	172.0	2.0	2.2	2.1
" "	Hvy.	5	993.2	3.1	5.3	4.0
Int. D-fir	Med.	3	149.1	1.1	2.7	2.1

[1]1 hectolitre = 2.75 bushels (Imp.) = 2.83 bushels (U.S.) approx.
[2]Clean, sacked cones from material delivered.

and they must be kept happy with a suitable wage, lots of cones to pick, and plenty of bug dope. Picker productivity may be enhanced where material has been hauled to a covered and cool central picking area.

The productivity data we have managed to collect so far provides what we think are fairly credible averages for at least the true firs and interior spruce (table 3). For other species, more information must yet be collected.

Good-sized collections of interior spruce have been made from both medium and heavy crops, and some evidence of the effect of crop abundance is beginning to emerge. We also found that productivity of clipping was higher, and costs lower, after formal training had been given to clipper operators.

At present, we are reasonably pleased with the progress made with aerial harvesting and we are confident that new developments will bring their rewards. The helicopter people have gained considerable experience and have learned a lot about cone picking. We feel that several of the carriers are capable and knowledgeable enough to undertake projects on their own. Accordingly, we are working with them to develop a contract document which will not only meet their needs but also serve the interests of their clients. We are sure that it will all work out just fine.

RECONDITIONING STRATIFIED SEED AT PINE RIDGE FOREST NURSERY

Katherine A. Yakimchuk

ABSTRACT: Lodgepole pine (Pinus contorta) and white spruce (Picea glauca) seed is stratified (moist, prechilling treatment) before sowing at Pine Ridge Forest Nursery, Alberta, Canada, to break dormancy and produce uniform germination. If any stratified seed remains after sowing it can be saved. It should be dried gradually to a storable moisture content (between 4 and 8 percent), placed in a sealed container, and stored at 0°F (-18°C) for later use. Stratified seed that has been reconditioned and stored has maintained its germinability and has produced strong, healthy seedlings.

INTRODUCTION

Lodgepole pine (Pinus contorta) and white spruce (Picea glauca) seed used for sowing at Pine Ridge Forest Nursery is stratified by a moist, prechilling treatment 3 weeks before sowing. Standard practice is to discard any seed remaining after sowing. The assumption is that this seed cannot be stored and maintain high quality. Seed has great value when stocks are low; therefore, it would be ideal to save this seed for future use.

Initial trials on reconditioning stratified seed at Pine Ridge Forest Nursery on five seedlots indicated little or no change in germination. The seedlots have retained their viability after being stored at 0°F (-18°C) for 4 years following stratification and reconditioning. The purpose of this paper is to describe tests of a procedure used for reconditioning stratified seed. This seed has maintained its germinability and has produced strong, healthy seedlings.

METHODS AND MATERIALS

Seed used for testing came from the seed inventory kept at Pine Ridge Forest Nursery. To perform this test, 10.5 ounces (300 grams) of seed were withdrawn from each seedlot. Ten white spruce and one lodgepole pine seedlots originating at various locations in Alberta (table 1) were tested. Germination and moisture tests were performed on the seed before stratification as a control.

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To stratify the seed it was first soaked in distilled water for 24 hours. It was then drained and each seedlot was placed in a plastic screen bag. The seed was spread in a thin layer to a depth of 0.25 inch (6 mm) inside each bag. The bags of seed were placed between layers of damp vermiculite in waxed cardboard boxes. Damp paper towelling was placed around the seed bags so vermiculite particles would not get mixed in with the seed. The seed was stored at 40°F (4.5°C) for 21 days. After 21 days the seed was removed from storage and a 0.5 ounce (15 gram) sample was taken from each seedlot for germination and moisture testing.

The remaining seed was air dried by pouring each seedlot out of its mesh bag onto a tray, and spreading it into a thin layer. An oscillating fan was placed by the seed to assist drying. The seed was dried for 15 to 20 minutes, until no surface moisture was visible. This is the condition of seed used in regular nursery sowing operations. A 0.5 ounce (15 grams) sample was taken from each seedlot for germination and moisture testing.

The seed remaining on the trays was left to dry for 3 days at room temperature, until it reached a storable moisture content of 6 to 8 percent. After this drying process, a 0.5 ounce (15 gram) sample was taken from each seedlot for germination and moisture testing.

Seed remaining was sealed in plastic bags and placed inside waxed cardboard boxes for storage in seed freezers at 0°F (-18°C). Following this the seed was sampled each month for germination and moisture testing to assess its quality.

Testing followed International Seed Testing Association rules (International Seed Testing Association 1976). Moisture content was analyzed using two 0.18 ounce (5 grams) replicates of seed each. The seed was oven dried at 220°F (105°C) for 16 hours. The percent moisture content was calculated on a wet-weight basis. Germination tests were made by placing the seed on moist kimpac paper towelling inside covered, clear, polycarbonate trays. Four replicates of 100 seeds each were used per test. Test seeds were germinated in Conviron germination cabinets for 21 days at 77°F (25°C) with a 12-hour photoperiod. Germination counts were made twice per week using the vigor class system developed by Wang (1973). During seedling evaluations, only the vigor class 1 seedlings were removed from the trays. The remaining seedlings were left to develop further.

Table 1.--Origins and collection years of seed samples used from the Alberta seed inventory for reconditioning tests

Seedlot	Species[1]	Collection year	Location: Township	Range	Meridian	Longitude (°W)	Latitude (°N)
1	Sw	79	110	16	5	116° 45'	58° 35'
2	Sw	75	94	11	4	111° 50'	57° 10'
3	Sw	82	80	25	4	114° 05'	55° 55'
4	Sw	83	80	25	4	114° 05'	55° 55'
5	Sw	79	77	11	6	119° 55'	55° 45'
6	Pl	82	66	10	5	115° 45'	54° 45'
7	Sw	79	62	20	5	117° 25'	54° 25'
8	Sw	82	43	10	5	115° 45'	52° 45'
9	Sw	79	41	15	5	116° 35'	52° 35'
10	Sw	79	35	8	5	119° 25'	52° 0'
11	Sw	71	8	4	5	114° 45'	49° 40'

[1]Sw = white spruce, Pl = lodgepole pine

Final germination percentages were calculated to a vigor class 4. At Pine Ridge Forest Nursery it is felt that a seedling not having reached this size in 21 days will not survive in the field or greenhouse. Vigor classes used are as follows:

1. Normal, fully developed seedlings with seedcoat completely shed.
2. Normal, well-developed seedlings with seedcoat almost shed.
3. Normal, well-developed seedlings with visible cotyledons and seedcoat partly shed.
4. Normal seedlings with moderately developed hypocotyl and cotyledons barely visible.

Analysis of variance was performed on the germination test data for each treatment. Germination percentages calculated to vigor class 4 and vigor class 2 were analysed. Duncan's multiple range test was run to test the differences in germination among treatments.

Visual assessments of seedling growth were made during seedling counts. These were based on height, strength, color, and uniformity of growth among all seedlings.

RESULTS AND DISCUSSION

Visual assessment showed that seedlings from the control (no treatment) for all seedlots were strong and healthy but showed an unevenness of growth. Heights of seedlings within each replicate varied. Seedlings from stratified seed showed uniformity in height and were generally tall, strong, and healthy. This was seen at the onset of the trial as well as after the seed had been kept in cold storage.

The initial moisture content of all but one seedlot was between 5 and 7 percent (table 2). After stratification, moisture contents increased to 31.4-34.5 percent. When the seed was air dried for removal of surface moisture, moisture contents were lowered to 28.6-32.2 percent. After air-drying the seed for 3 days, moisture contents were reduced to 5.9-7.7 percent. This is the recommended moisture content for long-term storage of white spruce and lodgepole pine seed (Wang 1974). The seed retained this moisture content during the time it was kept in storage.

Table 2.--Moisture content (percent) of 11 Alberta white spruce and lodgepole pine seedlots after four treatments

Seedlot	Control	Treatment: Wet	Air Dry	Dried for storage	Stored for 1 year
1	6.0	31.4	29.7	7.7	7.0
2	3.8	33.1	31.1	6.3	6.5
3	5.6	31.9	31.5	6.6	6.6
4	6.3	32.6	29.0	5.9	6.2
5	5.9	31.3	30.1	6.9	6.8
6	6.3	34.5	32.2	7.7	7.6
7	5.7	31.9	30.5	7.5	7.2
8	5.2	32.5	28.6	6.1	6.4
9	6.4	34.1	31.5	7.7	7.3
10	6.1	32.9	30.9	7.6	6.6
11	5.7	32.9	31.9	6.1	6.3

Analysis of variance at a 5 percent confidence level, based on germination results to a vigor class 4 and 2, indicated that eight of the 11 seedlots showed significant differences among treatments. In most of these cases, the control germination percentages are lower than those of the treated seeds. This indicated that stratification is necessary for maximum germination. Germination percentages varied very little among the stratified, air dried, and dried-for-storage trials. Sampling and testing the seed monthly while it was in storage indicated that the germination percentages for most of the seedlots remained very close to the original stratified percentages. For seven seedlots, the analysis of variance indicated there was a significant difference in germination in the last months of storage. Viability of the seed may have been deteriorating, but the seedlings produced from these seedlots were still very strong and healthy. Five of the seedlots that showed a reduction in germination had a lower germination percent originally. The other seedlots appear to be just as vigorous after being kept in storage as they were at the start of the trials.

By comparing germination percentages to vigor classes 2 and 4 (table 3), it is evident that the seed has retained its germination capacity, as the seed germinated quickly and reached an acceptable size in 21 days. The majority of the seedlings reached the vigor class 2 size within 21 days.

The germination data show that stratifying the seed, drying it, and storing it at 0°F (-18°C)

Table 3.--Comparison of germination (percent) of 11 Alberta white spruce and lodgepole pine seedlots after four treatments and seven storage times[a]

Seedlot	Control[b]	Wet[c]	Air Dry[d]	Dry[e]	Storage time (months) 2	3	4	5	6	7	8	9	10	11	12
GERMINATION TO VIGOR CLASS 4 IN 21 DAYS															
1	86^{2}	91	90	86	93	90	88	90	91	89.5	91	90.5	86^{7}	87^{1}	85^{6}
2	68^{6}	82	82	83	80.5	76.5	75	76	78.5	76	77.5	72^{3}	69^{5}	72^{3}	66.5^{6}
3	67^{2}	78.5	77	72	73	74	70.5	73	74.5	75	72	70^{1}	66^{2}	67^{2}	68^{2}
4	67^{4}	80	77	74	77.5	74	67.5^{4}	70.5^{1}	76	65^{6}	68^{4}	67.5^{4}	66.5^{4}	67^{4}	71^{1}
5	88.5^{11}	96	94	94	96	95	93	94.5	96	92	91^{3}	94	92	93	93
6	93	94.5	96	94	93	93	91	95	93	92	92	92.5	95	95	91
7	48.5^{14}	72	67	65	70.5	63^{1}	62^{2}	59^{2}	64.5	59^{2}	60^{2}	62.5^{1}	59.5^{2}	62^{2}	66
8	91.5^{8}	97	95	97	96	94	94	95	96	96.5	97	96	94.5	93^{2}	93^{3}
9	79	83	81	80.5	80	72^{5}	74^{1}	76	79	75^{1}	81.5	77.5	75^{1}	72^{6}	75^{1}
10	75	81	76.5	74.5	76	76	78	74	73	72	70	70	73.5	78	71
11	81	84	83	82	86	84	79	82	81.5	84	78	83	82.5	85	79
GERMINATION TO VIGOR CLASS 2 IN 21 DAYS															
1	80	90	90	85	91.5	87.5	85	88	90.5	86	86	88.5	83.5	85.75	82
2	52.5^{7}	64.5	60^{4}	68	74.5	66.5	58^{4}	59^{4}	71.5	72.5	72	45^{11}	51.5^{7}	61.0^{2}	46.75^{8}
3	60.5^{4}	71.5	74	69.5	67	71	68	68.5	71	68	67	65.25	58.75^{7}	61.75^{4}	64.75
4	59^{6}	77	74.5	72	73.5	70	64^{3}	67.5^{1}	72.5	64^{4}	66^{1}	61.25^{5}	61.5^{5}	62.25^{5}	65^{2}
5	83^{13}	94	93.5	93.5	94	93	91	91.5	94	88.5^{4}	87.5^{3}	89.5	89	93	90.25
6	92	93.5	95.5	93.5	92.5	92	91	94	92.5	89.5	91.5	92	94.75	94.5	89.75
7	46^{14}	64.5	64	62	68	57.5^{1}	57.5^{1}	53^{3}	61.5	55^{3}	56.5^{1}	54.25^{3}	54.5^{3}	57.25^{1}	60.75
8	90.5	95	95	95	94	90	91.5	93.5	95	94.5	94.5	92.25	92	92	93
9	71^{2}	80.5	80	78	78	71.5^{2}	72	70^{2}	77	72	78	72.5	71.75	67.75^{6}	71.5
10	64.5^{6}	77	76	72.5	75	72.5	74.5	67^{3}	69.5	64^{7}	63^{7}	68.5^{1}	68.75^{1}	74.5	65.25^{5}
11	69^{11}	80	81	80	83	81	73.5^{1}	79	80	81.5	75	78.25	78.75	79	73.5^{2}

[a]Raised numeral in table indicates number of times treatment is significantly lower than others in the trial at a 5 percent level determined by Duncan's multiple range test.
[b]No treatment.
[c]Stratified seed before air drying.
[d]Seed air dried for removal of surface moisture.
[e]Seed dried to a moisture content of 6-8 percent.

does not destroy seed quality. All seedlots reacted similarly, regardless of their origin in Alberta.

CONCLUSIONS

1. White spruce and lodgepole pine seed must be given a moist prechilling treatment before sowing, to attain maximum germination and uniform growth.
2. Stratified seed that has not been sown should be dried down gradually to a moisture content of about 6 percent, sealed in a container, and stored at $0^{o}F$ (-18^{o}).
3. Reconditioned seed should be used within 1 year to ensure high quality. Some seedlots may have lower germination, as determined by periodic testing, after being reconditioned and stored for several months. Seed should be used as soon as possible.
4. Seedlots that initially have lower germination potential deteriorate sooner than seedlots having high germination potential.
5. Saving unused stratified seed eliminates waste of costly seed, especially in areas where the seed inventory is low.
6. Testing will continue to determine whether reconditioned seed can be stored longer than 1 year and still maintain its viability.

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Section 3. Seed Orchard and Seed Production Area Management

REVIEW OF SEED PRODUCTION AREA AND SEED ORCHARD MANAGEMENT IN THE INLAND MOUNTAIN WEST

Jenji Konishi

ABSTRACT: Based on survey data from various agencies in the Inland Mountain West, which covers that region between the east slopes of the Cascade Mountains, the Rocky Mountains, through to the Plains, the current scale of the planting program is identified. The proportion of cones collected for various species from natural stands, seed production areas, and seed orchards is estimated.

Current practices in cone crop induction, cone and seed pest control, and cone harvest and processing methods employed to procure the necessary seed supply are reviewed.

The future trend for certain portions of the Inland Mountain West region is to establish and intensively manage seed orchards to produce seed of superior genetic quality for the major reforestation species.

INTRODUCTION

The area surveyed to address my topic includes the three (3) western Canadian provinces and thirteen (13) of the western and mid-western states of the United States (fig. 1). The area west of the Cascade Mountains has been excluded for the purposes of this review.

Within the Inland Mountain West Region the current annual planting program is estimated to total 201,681,000 trees. The total planting in the Canadian portion of the Region is 127,333,000 trees, and in the 13 states 74,348,000 trees (table 1).

This Region is characterized by diversity in climate, terrain, and economically important conifer tree species.

Paper presented at the Symposium on Conifer Tree Seed in the Inland Mountain West, Missoula, MT, August 5-6, 1985.

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Figure 1.--Inland Mountain West Region (The dashed line marks the divide of the Cascade Mountains).

The major species planted in the provinces are engelmann and white spruce, lodgepole pine, Douglas-fir and jack pine (table 2). The major species planted in the states are Engelmann spruce, Douglas-fir, ponderosa, lodgepole, white, and sugar pine, grand fir, and larch.

Table 1.--Production of tree planting stock for the Inland Mountain West Region

Region Area	Production	
USA (1984)		
Arizona	190,000	
California	10,000,000*	
Colorado	2,716,000	
Idaho	25,349,000	
Montana	2,643,000	
Nevada	237,000	
New Mexico	7,641,000	
North Dakota	3,558,000	
South Dakota	1,734,000	
Oregon	10,000,000*	
Washington	10,000,000*	
Utah	280,000	
Wyoming	No data	
Total 13 states		74,348,000
Canada (1985)		
British Columbia	87,000,000*	
Alberta	30,333,000	
Saskatchewan	10,000,000	
Total 3 provinces		127,333,000
Total estimated planting - Inland Mountain West Reg.		201,681,000

*Estimates for east of Cascades

For source of data see references.

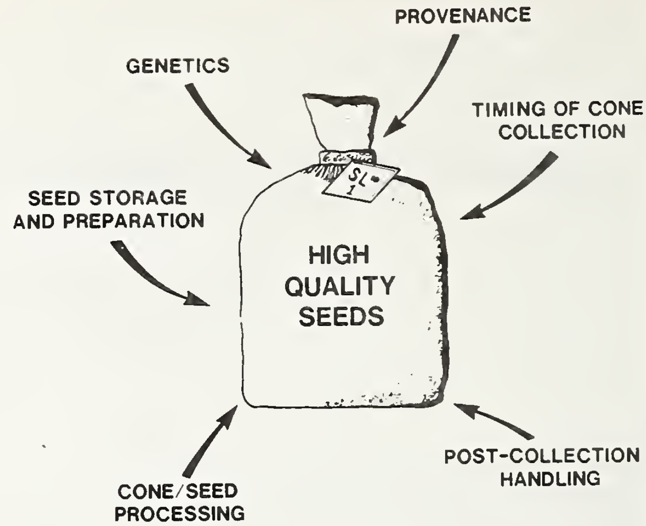

Figure 2.--Factors contributing to high seed quality.

For the provinces, based on the above species ratio and planting rate, a total of approximately 3405 hectolitres of cones (9,350 bushels) are required to annually sustain a program of this scale. These cone volumes do not consider needs of direct seeding programs in Alberta and Saskatchewan. Considering the species mix for the mid-western states it is estimated that an equivalent volume is needed to sustain the United States' portion of the program in this Region.

In order to meet the above demands a systematic approach to seed procurement was undertaken. It included the establishment and management of seed production areas (SPA's) and seed orchards. The objective of these concepts was to secure and provide high-quality seeds (fig. 2) needed for the expanding planting programs. In some of the species, collectible

Table 2.--Major species planted in western Canadian Provinces (millions of trees sown for in nurseries - 1985)

	Spruce (White & Engelmann)	Lodge-pole Pine	Douglas-fir	Jack Pine	Other Species[1]	Totals
B.C.[2]	56.5	22.0	5.1	-	3.4	87.0
Alberta[3]	26.0	4.2	0.1	-	-	30.3
Sask.[4]	6.3	-	-	3.7	-	10.0
Totals	88.8	26.2	5.2	3.7	3.4	127.3
	69.7%	20.6%	4.1%	2.9%	2.7%	100.0%

1 Other species includes Western Red Cedar, Western Larch, Western White Pine and Ponderosa Pine.
2 Silviculture Branch, Ministry of Forests, Province of B.C., Victoria. Excludes planting west of Cascade Mountains.
3 Reforestation and Reclamation Branch, Energy, Mines and Natural Resources, Province of Alberta, Edmonton.
4 Forestry Division, Parks and Renewable Resources, Province of Saskatchewan, Prince Albert.

cone crops occur at infrequent intervals in natural stands. For example, in British Columbia, seven collectible interior spruce cone crops have occurred during the past 26 years (fig. 3). This equates to a collectible crop every 3.7 years but experience indicates there can be intervals for up to 10 years between collectible crops. Cone crop periodicity in some species makes procurement of a sufficient inventory of seeds difficult.

SOURCES OF SEEDS

Over the past 20 years, most provinces, states and larger private land agencies within the region have established SPA's for the major planting species (Appendix I). In general, SPA's have been established to produce seed in the interval required to establish seed orchards and bring them into production.

Seed orchard programs have been implemented recently (within the last 10 years) in the interior region of B.C. and Alberta, and are in the planning stage in Saskatchewan. In the western states, orchards have been established in some areas for those species with larger planting demands (Appendix II). Over the next 10 - 20 years as established orchards mature and additional orchards are planted, this concept will significantly increase as a source of genetically improved seeds for future reforestation programs.

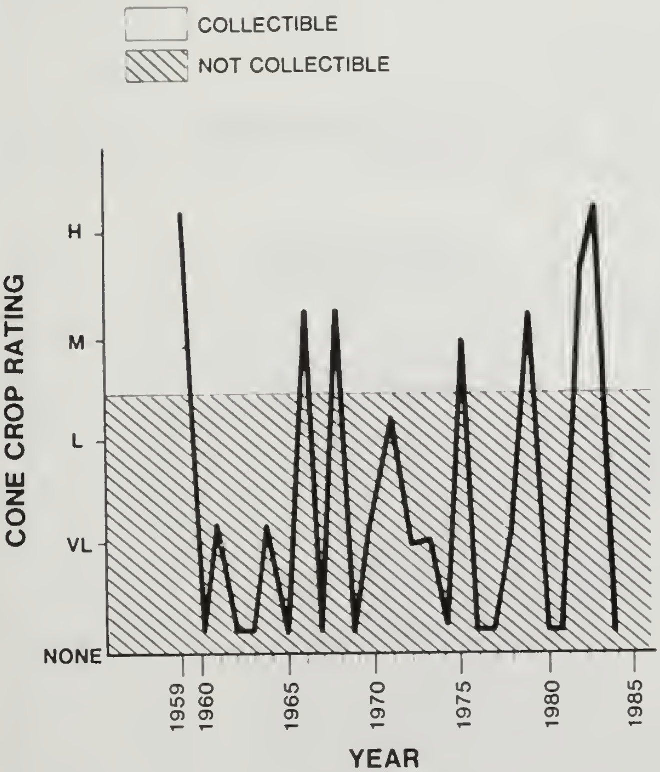

Figure 3.--Spruce cone crop rating 1959-1984, central interior region of British Columbia.

Based on a Canada-wide tree seed survey (for 1980-81) by P. S. Janas and B. D. Haddon over 88% of seed used for major reforestation species originated from unimproved natural stands, slightly over 11% came from seed collection and seed production areas and only 0.2% was from seed orchards. A similar pattern exists for the provinces within the Inland Mountain West Region. Data of this nature were not obtained from the Western States, but again, a similar distribution in terms of source of seeds is suspected.

In summarizing, despite the establishment of SPA's and orchards over the past 20 years, the majority of cone collections are currently being harvested from unmanaged natural stands.

In some provinces and states, provenance tests have been established and reviewed (10 years+ after establishment). For example, in B.C. a review of provenance tests for interior spruce and lodgepole pine has resulted in the revision of seed zonation and transfer rules as well as the identification of superior provenances to serve as priority areas for operational cone collection (figs. 4 and 5). It is of interest to note that in both spruce and lodgepole pine some of the best-performing provenances originated from low to middle elevation in the moist transition zone between the dry and wet interior forests west of the Rocky Mountains.

MANAGEMENT PRACTICES - SPA'S

Stand Selection

Stand selection has for the most part been done without the benefit of advance provenance testing work. Some of the criteria used for selection can be listed:

(a) thrifty young stands (25 - 30 years+) with good tree form,

(b) appropriate geographic and elevational distribution within a seed planning zone,

(c) gently sloping terrain and south facing aspects are preferred, and

(d) stand should be accessible by all weather road.

Roguing, Thinning, and Brush Control

Selected stands are brushed out to reduce weed competition and thinned and/or rogued of overstocked stems. Inferior phenotypes are removed to enable genetic improvement both within the SPA and within a perimeter buffer strip (usually 5 times the average tree height in width) to serve as a pollen isolation zone.

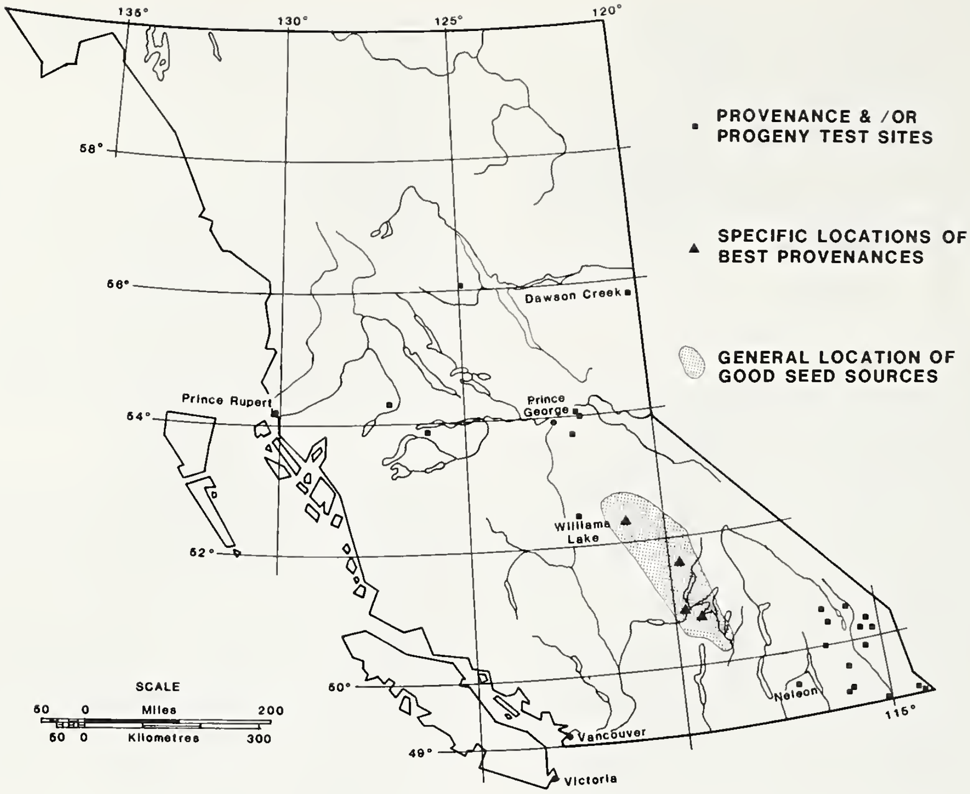

Figure 4.--Interior spruce provenance and progeny test sites and location of good seed sources.

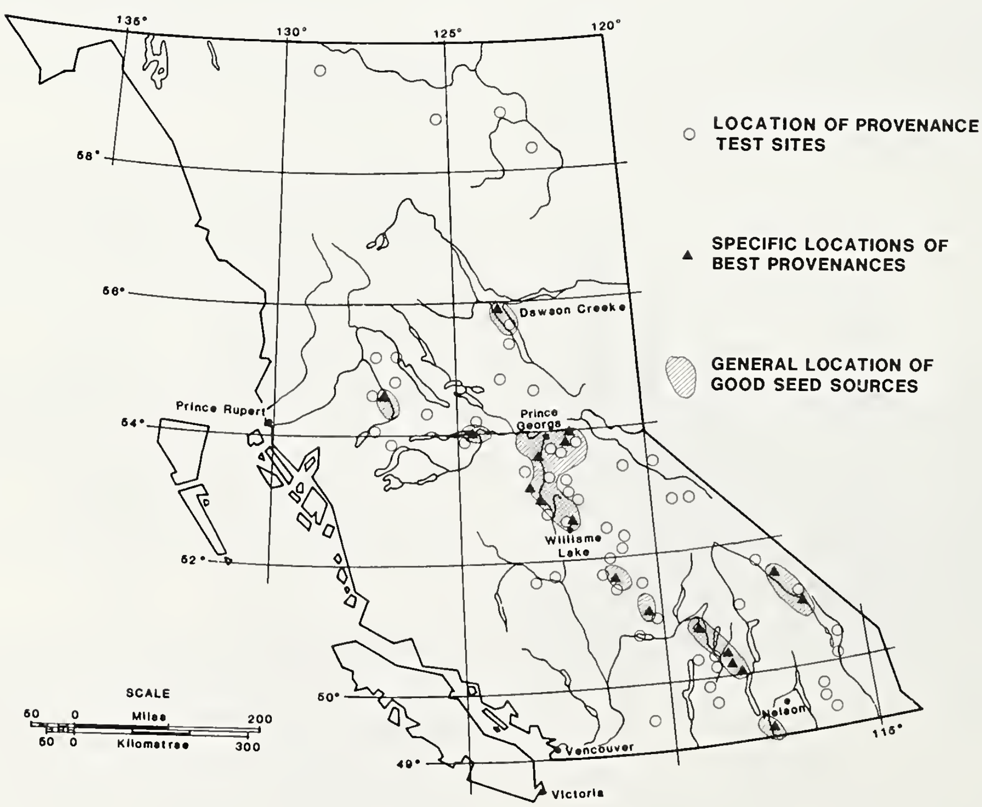

Figure 5.--Lodgepole pine provenance test sites and location of good seed sources.

In thinning, care needs to be exercised to prevent windthrow and sunscalding of residual trees.

Thinning provides for free growing trees which produce large crowns conducive for optimizing cone production. It also provides for access by equipment for cultural and protection operations.

Fertilizing

To improve the nutritional status of the soil and the trees and to induce cone production, fertilizer applications are made usually in the form of ammonium or calcium nitrate. Fertilizing is done manually, by tractor powered equipment, and in some instances, by aircraft. In British Columbia, despite fertilizing treatments in interior Douglas-fir and interior spruce SPA's the response in terms of cone induction has been inconsistent.

Protection

During brushing and thinning operations the resulting slash is disposed to reduce the fire hazard. It is also important that forest land management staff are advised of the location of SPA's so that they can be protected where possible from fires and/or land alienation for rights-of-ways or for other purposes.

Experiments to control cone and seed pests on SPA's have been limited and the results inconsistent.

Cone Harvest

Cone harvesting is usually done by climbing. In some SPA's where the trees have grown tall the tops have been removed at time of cone harvest.

Summary of Current SPA Performance

In some species such as ponderosa, lodgepole, and white pine, seed production from SPA's has been consistent. In many of the other major species such as engelmann and white spruce, Douglas-fir, and larch, production has been sporadic. In B.C. only one or two cone collections have been made from the interior spruce and Douglas-fir SPA's established 20 years ago. Where poor seed production has been experienced, the concept needs to be evaluated and perhaps phased out. In some instances it is doubtful that the costs of SPA establishment and management can be justified in light of the low seed production and limited genetic improvement resulting from this approach. In the survey, an attempt was made to gather seed yield data from SPA's. While many returns were received there exists a scarcity of yield data. This recent experience in data collection was also echoed previously (1974) by Paul Rudolph, Keith Dorman, Robert Hitt and Perry Plummer in Chapter III, Production of Genetically Improved Seeds, U.S. Woody Plant Seed Manual.

MANAGEMENT PRACTICES - SEED ORCHARDS

Planning

Where large scale planting programs are to be sustained over a long term, seed orchard programs have been implemented and/or are under consideration to provide both abundant quantities of seeds as well as superior genetic quality.

Long-term forecasting of species planting requirements (20 - 50+ years) is fundamental to priorizing tree breeding and seed orchard projects for a species. To optimize genetic gains it is essential that orchard programs be integrated with breeding programs.

Tree breeding and associated seed orchard programs represent a substantial long-term investment where the returns are not realized until harvest of the next forest crop. In view of this point, it is important when implementing a tree improvement program for a species that favourable cost-benefit studies be provided to ensure long-term and sustained support from financial authorities (i.e., Government or forest company).

Once the orchard project is decided upon further decisions must be made as to the type of orchard to establish (i.e., seedling vs. clonal). Experience in coastal Douglas-fir indicates that seedling orchards outproduce clonal orchards 2:1. The generation of orchard needs to be selected (1st vs. 1.5 vs. 2nd generation orchard). An orchard design must be prepared to define tree spacing and clonal or family arrangement to enable optimal panmixia. An orchard working plan document which covers the above topics as well as those which follow can aid orchard staff in management operations.

Within the region surveyed orchard management varies from extensive to intensive. The points which follow apply to intensive management.

Site Selection

Orchard site selection is of crucial importance in that it can determine the success or failure of the project. Some important factors to consider are listed:

(a) climate - warmer and drier site than that of the parent tree's site region. Avoid sites which are subject to late spring or early autumn frosts.

(b) soil and topography - well drained soils on level to very moderate sloping ground which can be easily worked by equipment should be selected. Avoid sites characterized by strong prevailing winds.

(c) services and economy of scale - to enable efficient management of the orchard the following points need to be considered:

   (i) availability of an abundant suitable water supply,

   (ii) good access road and close proximity to hydro, labour, equipment and supplies,

   (iii) plan for enough orchards to be located on a site to justify capital improvements; orchards in combination with nursery operations also assists in meeting economy of scale.

(d) freedom from pests - areas free of known pests and diseases should be selected. For example, root rots and tree rusts can cause problems.

(e) isolation - the site should be isolated from foreign pollen and also from residential areas and lakes or streams which may restrict use of pesticides within the orchard.

Irrigation

Most orchards are equipped with either drip or solid-set irrigation systems.

A drip system is cheaper than the overhead system and requires much less water. The irrigation line can be either laid on the surface or buried.

The solid set system can be used to cool the orchard in the spring and thereby delay the flowering of orchard stock. This delay in flowering can reduce pollen contamination (where the same species occurs adjacent to the orchard) as well as risks from frost and cone and seed insect damage.

Drainage, Site Preparation, and Cover Crop Establishment

The orchard site should include installation of water drainage systems where required. The soil should be well prepared prior to planting to permit good drainage and allow optimal root development. Establishment of a cover crop can aid in controlling erosion and reduce soil compaction and add organic matter.

Soil and Tissue Analysis and Fertilizer Prescriptions

Soil analysis should be completed early in the planning stage to determine nutrient status levels and pH. Examination should also be made for soilborne pests.

Soon after orchard stock is planted, twig and needle samples should be taken at a specific time each year (e.g. early October in B.C. orchards) and the tissue material analyzed at a laboratory. This data should then be interpreted to develop appropriate fertilizer prescriptions to keep orchard stock in a healthy and vigorous condition at all times.

Pruning

Pruning may include removal of small inter-nodal branches in some species to improve light penetration and aeration. Top pruning may be required to control height where orchard irrigation systems are installed and to minimize cone picking height.

Cone and Seed Pest Control

A sound knowledge of and the ability to identify pests at an early stage as well as availability of effective pesticides and control methods are basic to controlling loss of seeds from pests.

As cone and seed insects can be one of the major sources of seed loss, consideration should be given to organizing conelet sampling and analysis for each orchard to determine insect infestation levels as conelets develop. Accurate assays done at the right time can assist the orchardist in deciding whether to spray or not to spray for control.

Sanitation practices include picking all the cones from the trees regardless of crop size. Leaving cones on trees and allowing them to drop to the ground only serves as a brooding base to increase insect populations.

Pollen Handling

Techniques have been developed to harvest, extract, store, test, and reapply pollen on orchards. This enables improvement of the genetic makeup as well as yield of seeds, especially in the early phase of seed production. Once sufficient within-orchard pollen is produced wind pollination is sufficient, however, booster pollination to the very early and late flowering trees can optimize seed set. To be of benefit it is most important that pollen be applied when flowers are in the optimal receptivity phase of conelet development, (i.e., just after bud burst).

Cone Induction

While choosing the appropriate site for orchard location can provide abundant and frequent cone production, experience indicates that many trees in an orchard do not produce cones at the frequency and quantities desired. Consistent annual or biennial seed production of all trees is desirable.

Some treatments being used operationally and/or experimentally to induce cone production include root pruning, girdling, fertilizing, and application of gibberlic acids.

Cone Harvesting

Most cone harvesting in orchards is done with the aid of ladders. In some orchards, hydraulically operated man-lift units used in the fruit industry are also utilized in seed orchards. These units have a slow ground speed but are versatile in that they can be used for conducting orchard surveys, enable pruning, pest control and pollination as well as for cone harvest.

Alternatives to Conventional Orchards

Field orchards require careful site selection, investment in land area sufficient to enable economy of scale of operations and 10 - 15 years are required prior to production of significant quantities of seeds. Container-based seed orchards in greenhouses can accelerate abundant and early seed production, reduce the land area required and may be a cost effective alternative to field-based orchards.

Another alternative is hedging orchards whereby selected superior clones are established in hedges to serve as cuttings for asexual production of planting stock.

Summary of Current Orchard Programs and Performance

In the provinces, orchards are in the very early stage of production and many orchards are under development or in the planning stage. Early production experience in lodgepole pine indicates that orchards can consistently produce seeds germinating at 95%+ and the seeds are larger than those from natural stands. In the North Idaho and Montana area most of the seed production to date is rust resistant white pine. Many other orchards are established or under development for the other major reforestation species. Based on survey returns orchards have not yet been established in Colorado, South Dakota, Wyoming, Arizona, New Mexico, Utah and Nevada. In these states the scales of the planting programs are considered too small to develop an economic tree improvement and orchard program. Also, for this area, much reliance is placed on natural regeneration. In the Pacific-northwest area (east of Cascade Mountains) in Washington and Oregon the main production to date has been in blister rust resistant white pine. Early seed production is being experienced in grand fir, Shasta and white fir, larch, ponderosa, sugar, and lodgepole pine, and many orchards are in the development stage. In this area it is intended that as seed orchards produce sufficient seeds to meet program needs the SPA's will be phased out.

It is most important that seed orchard programs be integrated with tree breeding programs and/or utilize the information provided by thorough provenance studies for a species. In this way maximum genetic improvement of the seed produced is realized.

While many seed orchard management practices have been developed during the past 20 years there exist opportunities for improvement in the following areas:

- genetic quality improvement through early establishment of 1.5 or 2nd generation orchards linked to long-term breeding plans,
- carefully evaluate the performance of 1st generation orchards and from this experience make improvements in orchard site selection, and in design of 1.5 or 2nd generation orchards so that both genetic gain and seed productivity is optimized,
- a significant increase in orchard development and establishment is needed forthwith if orchard seed is to be the major source of seeds for future planting programs,
- expediting earlier seed production through development of new techniques such as containerized orchards,
- establishment of hedging orchards which serve to produce rooted cuttings,
- research is required on cone induction to ensure that all trees produce abundant and regular crops, and
- research is required on pests and their control to minimize loss in orchards.

ACKNOWLEDGMENTS AND CONCLUDING REMARKS

In concluding I wish to thank the organizers of this important symposium for the opportunity to review SPA and seed orchard management in the Inland Mountain West. I also wish to thank those persons who responded to my questionnaire on SPA's and seed orchards. I am sure this symposium and the resulting proceedings will contribute most significantly towards extending knowledge of seed biology, of operational cone collection and seed handling practices as well as management of SPA's and seed orchards. I cannot overemphasize the importance of knowledgeable, well-trained, enthusiastic and dedicated silviculture staff in meeting the objective of supplying high-quality seed for forest renewal programs.

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APPENDIX I

Inland Mountain West Seed Production Areas (SPA's)

Species[a]	No. SPA's	Area (ha/ac)	Seed Produced to Date (kgs/lbs)	Ave. Annual Amount Seed Production (kgs/lbs)	Agency
CANADA - (Metric)					
British Columbia (East of Cascades)					
Fdi	21	-	-	-	MOF
Lw	1	-	-	-	MOF
Py	2	3949.2	-	-	MOF
Pw	1	-	-	-	MOF
Pl	2	-	-	-	MOF
Se	9	-	-	-	MOF
Sx	53	3478.3	-	-	MOF
Totals:	89	7427.5	[b]		
Alberta					
No SPA's considered to be active.					Government
Saskatchewan					
Sw	5	52.0	15.6	4.0	Government
Grand Total Western Provinces	94	7479.5	-	-	
USA - (Imperial)					
Region 1 - Northern Region - USDA (N. Idaho, W. &. Cen. Montana)					
Fdi			57.4	14.4	Nat. Forest
Lw			4.6	1.2	Nat. Forest
Pw	40[c]	842	85.1	21.3	Nat. Forest
Pl			11.8	2.9	Nat. Forest
Pw	1	6	0.0	0.0	Montana State
Totals:	41	848	158.9		
Region 2 - Rocky Mountain Region - USDA (Colorado, South Dakota, Wyoming)					
Py	5	95	535	134	Wyoming State
Pl	1	4	0	0	Colorado State
Py	1	142	-	-	Nat. Forest
Py	1	40	-	10.4	Nat. Forest
Totals:	8	281			

[a] See Appendix III for species abbreviations.
[b] Minimal collections made each year.
[c] Fdi and Lw will predominate.

APPENDIX I (Cont'd)

Inland Mountain West Seed Production Areas (SPA's)

Species	No. SPA's	Area (ha/ac)	Seed Produced to Date (kgs/lbs)	Ave. Annual Amount Seed Production (kgs/lbs)	Agency
USA - (Imperial)					
Region 3 - Southwestern Region - USDA (Arizona, New Mexico)					
No SPA's - candidate areas are anticipated to be submitted for review and approval in the next few years.					
Region 4 - Intermountain Region - USDA (S. Idaho, Utah, Nevada)					
Fdi	2	18	-	-	Nat. Forest
Py	11	100	-	-	Nat. Forest
Pl	1	-	-	-	Nat. Forest
Totals:	14	118			
Region 6 - Pacific Northwest Region - USDA (Washington, Oregon - East of Cascades)					
Lw	5	22	-	-	Nat. Forest
Py	2	5	-	-	Nat. Forest
Pl	1	22	-	-	Nat. Forest
Se	1	15	-	-	Nat. Forest
Totals:	9	64			
Grand Total USA	72	1311			
Grand Total Inland Mountain West (Can. & USA)	166				

APPENDIX II

Inland Mountain West Seed Orchards

Species	Stage of Orchards[a] (No. - ha/ac) Dev.	Est.	Prod.	Totals	Total Seed Produced to Date (kgs/lbs)	Ave. Ann. Cur. Seed Production (kgs/lbs)	Agency
CANADA - (Metric)							
British Columbia (East of Cascades)							
Pli	2- 8.6	4-14.7	-	6-23.3	5.62	1.87	MOF
	1- 5.0		-	1- 5.0	-	-	Co-op.[b]
Sx	2- 7.7	8-23.6	-	10-31.3	2.32	-	MOF
	1- 7.4	2- 5.6	-	3-13.0	-	-	Co-op.
Totals:	6-28.7	14-43.9	-	20-72.6			
Alberta							
Pl	1-14.7		-	1-14.7	-	-	Co-op.
Sw	2- 3.5	1- 2.5	-	3- 6.0			Co-op/F.S.
Totals:	3-18.2	1- 2.5		4-20.7			
Saskatchewan							
No Seed Orchards established to date.							
Grand Total Western Provinces	9-46.4	15-46.4	-	24-93.3			
USA - (Imperial)							
Region 1 - Northern Region - USDA (N. Idaho, W & Cen. Montana)							
Fdi	5-37	-	-	5- 37	0	-	Nat. Forest
Bg	-	2- 30	-	2- 30	0		Nat. Forest
Lw	1-10	2- 24	-	3- 34	1.5		Nat. Forest
Py	-	4- 80	-	4- 80	0		Nat. Forest
Pw	1- 4	1- 16	5-80	7-100	275	40	Nat. Forest
Pl	2-20	-	-	2- 20	0		Nat. Forest
Py	-	1- 12	-	1- 12	few cones	-	B.of L.M.[c]
Fdi	1-12	-	-	1- 12	0		State Forest
Lw	1- 8	-	-	1- 8	0		State Forest
Py	-	1- 12.5	-	1- 12.5	0		State Forest
Blue Spruce	1- 3	-	-	1- 3	0		State Forest
d	1- 3	-	-	1- 3	0		State Forest
Totals:	13-97	11-174.5	5-80	29-351.5	276.5		

[a] Classification — Stage
- Developing — site clearing or preparation and/or under propagation.
- Established — 80%+ planted.
- Producing — orchards that have produced greater than 40% of seed target in any one year.

[b] Co-op = in British Columbia, cooperative seed orchards managed by forest companies under government funding.

[c] Bureau of Land Management.

[d] Russian Olive, Siberian Elm, Green Ash.

APPENDIX II (Cont'd)

Inland Mountain West Seed Orchards

Species	Stage of Orchards[a] (No. - ha/ac) Dev.	Est.	Prod.	Totals	Total Seed Produced to Date (kgs/lbs)	Ave. Ann. Cur. Seed Production (kgs/lbs)	Agency
USA - (Imperial)							
Region 2 - Rocky Mountain Region - USDA (Colorado, South Dakota, Wyoming)							
No established Seed Orchards in these states.							
Region 3 - Southwestern Region - USDA (Arizona, New Mexico)							
No known Seed Orchards in the private sector, or municipalites of New Mexico or Arizona.							
Region 4 - Intermountain Region - USDA (S. Idaho, Utah, Nevada)							
No Seed Orchards established.							
Region 6 - Pacific Northwest - USDA (Washington, Oregon - East of Cascades)							
Fdc	48- 465	-	-	48- 465	2898	3.4	Nat. Forest
Bg	3- 27	-	-	3- 27	-	8.9	Nat. Forest
Bsr	1- 9	1- 12	-	2- 21	-	6.8	Nat. Forest
Bw	9- 134	2- 14	-	11- 148	-	5.5	Nat. Forest
Lw	16- 172	-	-	16- 172	-	1.3	Nat. Forest
Py	51- 927	8-110	-	59-1037	-	8.9	Nat. Forest
Pw	8- 91	1- 10	-	9- 101	426	13.1	Nat. Forest
Pl	25- 351	1- 11	-	26- 362	-	2.4	Nat. Forest
Ps	2- 34	-	-	2- 34	-	21.6	Nat. Forest
Se	1- 7	-	-	1- 7	-	3.7	Nat. Forest
Ci	4- 38	-	-	4- 38	-	4.7	Nat. Forest
Fdi	-	1- 45	-	1- 45	0	0	Private Land
Py	-	1- 20	-	1- 20	0	0	Private Land
Fdi	-	1- 8	-	1- 8	0	0	State Forest
Totals:	168-2255	16-230	-	184-2485			
Grand Total USA	181-2352	27-404.5	5-80	213-2836.5			
Grand Total Inland Mountain West (Canada & USA)	190	42	5	237			

[a] Classification — Stage
- Developing — site clearing or preparation and/or under propagation.
- Established — 80%+ planted.
- Producing — orchards that have produced greater than 40% of seed target in any one year.

APPENDIX III

List of Species Abbreviations

Fdc	Douglas-fir (coast)	*Pseudotsuga menziesii* (Mirb.)
Fdi	Douglas-fir (interior)	Franco var. *menziesii*
Lw	Western larch	*Larix occidentalis* Nutt.
Py	Ponderosa pine	*Pinus ponderosa* Laws.
Pw	Western white pine	*Pinus monticola* Dougl.
Pl	Lodgepole pine	*Pinus contorta* var. *latifolia*
Se	Engelmann spruce	*Picea engelmannii* (Parry) Engelm.
Sx	Interior spruce (commonly white x engelmann hybrids)	*Picea* sp.
Sw	White spruce	*Picea glauca* (Moench.) Voss
Bg	Grand fir	*Abies grandis* (Dougl.) Lindl.
Bsr	Shasta red fir	*Abies magnifica* var. *shastatensis* Lemm.
Bw	White fir	*Abies concolor* (Gorde & Glend.) Lindl.
Ps	Sugar pine	*Pinus labertiana* Dougl.
Ci	Incense cedar	*Libocedrus decurrens* Torr.

PRODUCTION OF IMPROVED WESTERN WHITE PINE AND DOUGLAS-FIR AT POTLATCH CORPORATION'S CHERRYLANE SEED ORCHARD

Roger L. Blair

ABSTRACT: Potlatch Corporation's tree improvement program includes grafted seed orchards for western white pine and Douglas-fir. Production of improved seed at these facilities is discussed in light of the attributes of the orchard site, cultural procedures designed to promote early and consistent seed production, and supplemental mass pollination. Implications of orchard planting design are discussed as they affect production of white pine seed with varying degrees of rust resistance and Douglas-fir seed adapted to a range of elevational zones.

INTRODUCTION

Potlatch Corporation's Western Division began its artificial regeneration program in 1979. At that time the first crop from the Lewiston seedling production facility was outplanted. Since then the regeneration program has grown to the production of 1.8 million seedlings per year sufficient to regenerate 4,000 acres with present planting spacings.

Prior to beginning the artificial regeneration program, an extensive planning process indicated that sufficient acres of Douglas-fir and rust-resistant white pine would be planted to justify tree improvement programs in these species. Based on an evaluation of programs elsewhere and existing research data, we decided to develop the grafted seed orchard of both species on a carefully chosen seed orchard site.

LOCATION

The site on which the seed orchard is located is critical to its long-term capabilities of high, consistent cone production (Werner 1975). Experience in the Southeast and Pacific Coast as well as in New Zealand has indicated that the following factors contribute to a good seed orchard location:

1. Warm, dry climate. Sweet (1975) summarizes regional differences in flowering by indicating that high annual flower production and reduced periodicity appear to be associated with hot, dry summers. Searching for sites with these characteristics has become a major factor in seed orchard siting in the Pacific Northwest. In addition to the promotion of abundant flowering, the frequency of flower-damaging late spring frosts is greatly reduced or even eliminated. Potlatch Corporation's Cherrylane site is located in the Clearwater River valley east of Lewiston, Idaho. Annual precipitation is about 30 cm with typically hot, dry summers. The growing season is substantially longer than that which occurs at the elevations where white pine is native.

2. Isolation from natural stands. Although this site is well within the latitudinal and longitudinal boundaries of the ranges of interior Douglas-fir and western white pine, the site is remote by several kilometers from natural occurrence of either species. This will greatly reduce the potential for pollen contamination from unimproved surrounding trees, a factor particularly important for western white pine where blister rust resistance is critical. In addition, cone and seed damaging insects should be much easier to control without an uncontrolled population in surrounding stands (see Haverty and Shea, this publication).

3. Fertile, well-drained soils. While the sites upon which cone production is best do not always support maximum vegetative growth, good fertility is required for successful orchard establishment and good early vegetative growth. The Cherrylane site is a sandy loam which had been farmed for many years prior to orchard establishment. Soil pH is about 5.5, satisfactory for conifer growth. The site is adjacent to the Clearwater River and is hence alluvial in nature. At a depth of one to two meters, the soil grades to nearly pure river sand. These soil characteristics allow the soil moisture regime to be maintained at nearly any desired level with the existing irrigation system. Nutrients can be added or withheld as needed.

Paper presented at the Conifer Tree Seed in the Inland Mountain West Symposium, Missoula, MT, August 5-6, 1985.

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LAYOUT

Since the orchard is located in a deep, narrow valley, wind currents are greatly influenced by

topography. Although large weather systems can cause unpredictable wind direction, the more usual air drainage pattern is downriver, east to west. The orchard has been laid out to utilize these wind patterns (see figure 1). For example, in establishing a small section of a Douglas-fir seedling seed orchard, a gradient was utilized from low elevation seed sources to high elevation from the northern boundary of the orchard to the southern boundary. Given that most pollination occurs among neighboring trees, one can reforest sites with differing elevations with seed collected from the appropriate area of the orchard.

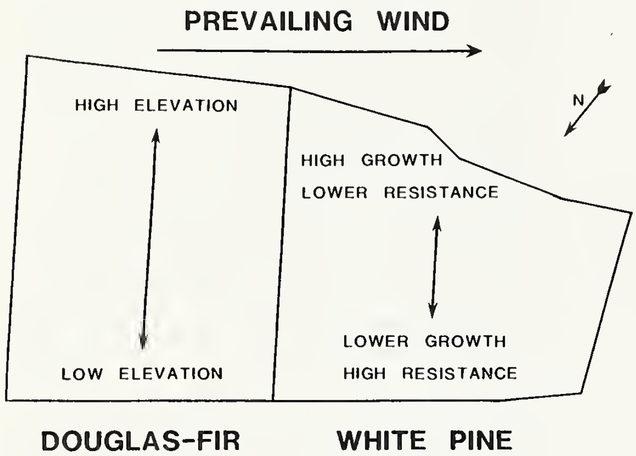

Figure 1.--Use of prevailing wind flow patterns in orchard design at Potlatch Corporation's Cherrylane Seed Orchard.

This layout procedure can be applied to other characteristics. For example, as data on rust resistance become available for our western white pine selections, a gradient from high resistance (with less emphasis on growth and form) to lower resistance (with more emphasis on growth and form) will be established across the seed orchard. This will be accomplished through the roguing process in the existing orchard and in the establishment of new orchard sections. Once again seed can be collected from the appropriate area in the orchard to match the requirement of the planting site. Sites known to be particularly high in rust hazard can be reforested with seed of maximum resistance. This procedure maximizes the utilization of expensive seed orchard sites (Blair 1983).

MANAGEMENT

Irrigation

Because of the orchard location and soil type, irrigation is essential for orchard establishment and maintenance. An irrigation system, utilizing overhead impact irrigation heads, was in place for the farming operation. This system was utilized during the first few years of orchard establishment and growth. This system soon became inadequate because of the labor-intensive nature of the movable pipe system, the interception of irrigation water by the developing crowns and the added cost of continued vegetation control with the broadcast irrigation.

The system has been replaced with a drip system designed to provide up to three gallons per hour per tree. With the orchard in full production, this system is sized to have the capacity to provide 18 gallons per tree per day. As the orchard is thinned and rogued, individual trees can be provided more water if needed.

An unforeseen problem with the drip system was the development of slime mold in the system and hence plugging of the emitters. Because water moves slowly through the drip irrigation pipes, incubation conditions for the slime mold organism were right for rapid proliferation. This problem has been corrected by injection of chlorine in the final stages of an irrigation set.

Fertilization

Both broadcast and individual tree fertilization have been conducted during the early stages of orchard establishment and growth. These methods were utilized during the period when overhead irrigation was in place. Injection of liquid fertilizers is now being accomplished through the drip irrigation system. The present fertilization regime is designed to maximize vegetative growth and uses a complete fertilizer (12-8-4, NPK).

Fertilization has long been known to improve cone production in western white pine (Barnes 1969). Timing and formulations of fertilizers and their interaction with irrigation are not well understood, particularly for site conditions similar to those at the Cherrylane Orchard. Cooperative research on this subject is planned for 1986.

Supplemental Mass Pollination

Seed cone production has been early and consistent on many of the 60 clones in the white pine seed orchard. Seed cone counts conducted in the spring of 1985 showed that 44 of the 60 clones were flowering by four years after grafting. An average of nine seed cones per tree were produced.

A major, but not unexpected, problem has been pollen production. Only a few of the 60 clones have produced pollen in significant amounts. To offset this imbalance, supplemental mass pollination experimentation was begun this year. Pollen collected at the U.S. Forest Service white pine arboretum in Moscow, Idaho, in the spring of 1984, was utilized. This pollen was collected from individuals known to be resistant to blister rust. An assembly used to inject a flux (powdered metal) into an air stream (a system used in gas welding) was modified to inject pollen. Commercially available high pressure nitrogen cylinders were utilized as a compressed air source. Air flow was directed at a seed cone cluster at 18 pounds per square inch. Although hampered by cool, wet weather, this device worked well mechanically and was exceptionally efficient in the use of pollen. Over 1400 flowers were pollinated, most two or three times, utilizing less than a pint of pollen.

Supplemental mass pollination offers the opportunity to control pollen source as well as to improve flower set and seeds per cone. This technology may be extremely important for western white pine where maximum blister rust resistance is required on many sites for successful plantation establishment.

SUMMARY

The Cherrylane Seed Orchard is believed to be ideally located for consistent high production of improved white pine and Douglas-fir seed. Although orchard establishment did not begin until 1979, preliminary indications are that early and consistent flower production will result. Orchard management is simplified by the location and soil conditions.

Orchard layout is designed to utilize prevailing airflow patterns to produce seed tailored for the site requirements. Supplemental mass pollination should speed our ability to produce seed in higher quantities and with desired characteristics.

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295 POTENTIAL AND ACTUAL SEED YIELDS FROM

A SOUTHERN PINE SEED ORCHARD

David L. Bramlett

ABSTRACT.--Monitoring the seed production on 26 sample trees in a loblolly pine (Pinus taeda L.) seed orchard in Georgia indicated that only 18.6 percent of the potential seed crop was recovered. Cone survival of the initial flower crop steadily decreased during the 18-month observation period, with an October 1978 cone efficiency of 0.585 of the original 1977 flower crop. Seed yields per cone were lower than expected for loblolly orchards and averaged only 50.4 filled seeds per cone and a seed efficiency of 0.375. Extraction efficiency and germination efficiency averaged 0.833 and 0.868, respectively. Seed yields from this orchard could be increased by increasing the size of the potential seed crop (flowers) or by increasing the overall seed orchard efficiency. Results indicate that a more intensive pest management program would reduce cone and seed losses and substantially increase seed orchard yields.

INTRODUCTION

To effectively and efficiently produce high levels of viable seed in southern pine orchards, managers need to have an accurate inventory of the annual seed production potential, and need to monitor the actual percentage of the seed crop that is harvested. An inventory-monitoring system (IMS) is currently being used in Federal, State, and industrial seed orchards (Bramlett and Godbee 1982). The system utilizes sample trees to quantify total flower production in the orchard and sample branches to periodically track the developing cone crop.

The use of IMS allows seed orchard managers to effectively allocate cone harvesting labor and equipment and to efficiently manage a pest control program on a cost-benefit basis. Effective and efficient management of seed orchards means that seed yields can be increased and that more genetically improved southern pine seedlings will be available for planting.

Paper presented at the Conifer Tree Seed in the Inland Mountain West Symposium, Missoula, MT, August 5-6, 1985.

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METHODS

Twenty-six loblolly pine (Pinus taeda L.) sample trees were selected in the Georgia Kraft Piedmont Seed Orchard, Greensboro, GA. Sample trees were randomly selected by row and column designations without prior visual inspection. The sample trees averaged 18 cm in diameter and 8.8 m tall. Tree ages ranged from 8 to 12 years old, with an average age of 10 years. In April 1977, approximately 2 weeks after female flower receptivity, the total flower count, including all healthy, damaged, or dead strobili, was tallied for each sample tree. At the time of the total flower count, eight sample branches were tagged and their initial flower count recorded as both healthy and dead flowers. The sample branches were distributed throughout the tree crown but were not randomly selected locations.

After the initial count, additional counts of all live flowers, conelets, or cones on the sample branches were completed in July and October of 1977 and in April, July, and October 1978. Mature cones were harvested from the whole tree in October of 1978 and classified as healthy, damaged, or dead. A cone analysis (Bramlett and others 1978) was completed on 10 random cones from each ramet. In the cone analysis the following properties of individual cones were observed: fertile scales, aborted ovules, total seed, filled seed, and germinated seed. Values of seed potential (SP), seed efficiency (SE), extraction efficiency (EE), and germination efficiency (GE), were calculated for each cone.

RESULTS

Flower and cone production data are presented in table 1. For the 26 sample trees, the total flower count ranged from 80 to 1,534, with a mean value of 444 flowers per tree. On the sample trees a total of 3,660 flowers were tagged for the periodic sample branch observations. The original flower count decreased with time from April 1977 to October 1978. Individual trees had varying survival rates ranging from 26.7 to 82.9 percent of the original flower count, with an overall average of 58.5 percent.

A similar observation of cone survival could be generated by comparing the total number of healthy cones harvested to the total number of flowers. For the 26 study trees an average of 63.4 percent of the flowers were harvested as mature cones. A regression (R^2 = 0.67) of the observations demonstrated a highly significant (P = .001) regression equation as follows:

Table 1.--Total flower count per sample tree and survival of flowers on branches from April 1977 through October 1978

Sample tree	Total flowers	Sample flowers	Survival year 1 Apr	July	Oct	Survival year 2 April	July	Oct
1	1,534	217	213	213	213	210	173	125
2	514	165	163	160	153	146	135	102
3	440	140	136	128	126	118	88	53
4	1,256	222	207	202	201	200	193	184
5	609	153	141	139	132	131	98	85
6	602	157	148	146	142	142	125	99
7	301	149	139	129	126	126	115	103
8	203	100	88	79	67	63	63	57
9	551	199	196	192	192	187	170	133
10	581	188	170	148	138	130	120	102
11	319	144	119	109	106	97	95	87
12	94	90	80	73	70	65	65	55
13	325	146	133	115	107	104	72	39
14	536	245	232	215	200	180	162	140
15	190	101	99	96	82	78	76	53
16	80	67	63	62	56	49	49	46
17	115	84	80	77	75	74	69	62
18	83	64	63	62	62	62	47	42
19	674	83	81	65	62	60	55	44
20	572	164	162	158	149	148	135	125
21	143	110	98	100	54	49	46	37
22	801	183	167	135	106	100	97	92
23	130	112	97	96	89	89	89	81
24	113	86	78	69	68	68	63	63
25	267	131	128	81	73	69	59	39
26	515	160	148	128	120	114	105	95
Sum	22,548	3,660	3,429	3,177	2,969	2,859	2,564	2,143
Mean	444	141	132	122	114	110	99	82

TREECE = 0.088 + 0.933 x OCT2CE

Where:

TREECE = total healthy cones (whole tree) divided by total flowers (whole tree)

OCT2CE = Total healthy cones (sample branches) divided by total flowers (sample branches)

A more useful relationship for the orchard manager would be to predict the number of healthy cones (PREDCONES) based on the observed total tree flower count (TOTALFLO) and the sample branch cone survival for the tree (OCT2CE).

Thus: PREDCONE = TOTALFLO x OCT2CE

Actual observations from the 26 sample trees indicated a very strong relationship between the total cone production per tree (TOTCONE) and the calculated PREDCONE value. No statistically significant differences were present between the mean values of PREDCONE and TOTCONE for the 26 sample trees in this study. A very highly significant relationship ($R^2 = 0.97$) can be described by the regression equation:

TOTCONE = 20.88 + 0.9612 x PREDCONE

Results of the cone analysis indicated that only an average of 50.35 filled seeds were produced per cone from the 260 sample cones (table 2). The seed efficiency calculated by the filled seeds per cone by the seed potential (Bramlett and others 1978) averaged 0.376 for the sample cones. Extraction efficiency calculated by dividing the number of extracted seeds by the total number of seeds per cone averaged 0.833. Germination efficiency was calculated as the number of filled seed per cone germinating in a laboratory test divided by the total number of filled seed per cone. The average observed value was 0.868.

With the four major components of seed orchard monitoring--CE, SE, EE, and GE--an overall seed orchard-to-nursery efficiency value (SO-NE) can be calculated as a product of the four parameters:

SO-NE = CE x SE x EE x GE

The average efficiency values for each tree are shown in table 3.

Table 2.--Cone analysis of 260 loblolly pine cones from Georgia Kraft Piedmont Seed Orchard, Greensboro, GA

Variable	Mean	Standard deviation
Cone length (mm)	82.13	13.08
Cone width (mm)	38.22	3.93
Fertile scales (no.)	66.00	10.47
First yr. aborted ovules (no.)	54.06	29.42
Second yr. aborted ovules (no.)	4.95	8.73
Extracted seed (no.)	64.33	38.03
Total seed (no.)	73.00	37.28
Filled seed (no.)	50.35	32.82
Empty seed	22.65	76.73
Germinated seed (no.)	46.92	32.89
Seed potential (no.)	132.01	20.95
Seed efficiency (SE)	0.376	0.23
Extraction efficiency (EE)	0.833	0.21
Germination efficiency (GE)	0.868	0.25

Table 3.--Values for cone efficiency (CE), seed efficiency (SE), extraction efficiency (EE), germination efficiency (GE), and seed orchard-to-nursery efficiency (SO-NE) for individual loblolly pine sample trees in the Georgia Kraft Piedmont Seed Orchard, Greensboro, GA

Sample tree	Efficiency value				
	CE	SE	EE	GE	SO-NE
1	0.576	0.728	0.984	0.997	0.411
2	0.618	0.684	0.972	0.973	0.400
3	0.379	0.583	0.933	0.906	0.187
4	0.829	0.425	0.985	0.988	0.343
5	0.556	0.485	0.968	0.979	0.255
6	0.631	0.490	0.901	0.858	0.239
7	0.691	0.399	0.963	0.995	0.264
8	0.570	0.599	0.957	0.958	0.313
9	0.668	0.378	0.816	0.982	0.203
10	0.543	0.338	0.763	0.912	0.127
11	0.604	0.234	0.826	0.779	0.091
12	0.611	0.100	0.478	0.915	0.027
13	0.267	0.177	0.780	0.947	0.034
14	0.571	0.173	0.807	0.949	0.076
15	0.525	0.060	0.520	0.212	0.003
16	0.687	0.042	0.519	0.496	0.007
17	0.738	0.329	0.932	0.969	0.219
18	0.656	0.412	0.639	0.950	0.164
19	0.530	0.480	0.754	0.785	0.151
20	0.762	0.715	0.938	0.934	0.478
21	0.336	0.290	0.924	0.909	0.082
22	0.503	0.328	0.878	0.905	0.131
23	0.723	0.226	0.891	0.386	0.056
24	0.733	0.537	0.916	0.989	0.357
25	0.298	0.262	0.695	0.929	0.050
26	0.594	0.291	0.909	1.000	0.157
Mean	0.585	0.376	0.833	0.869	0.186

DISCUSSION

A mean CE of 0.585 indicates that only 58 percent of the potential cone crop produced healthy cones. Although the monitoring system does not quantify specific causes of cone loss, observations during the periodic counts are used to identify the types of cone loss. Insects are generally the major cause of cone mortality, but fungal, environmental, and physiological causes are also known to cause mortality of loblolly pine flowers, conelets, or cones. The observed CE value for the 1978 cone crop appears to be about average for moderately protected loblolly pine seed orchards. Certainly the cone survival could be improved by increasing the degree of protection in the orchard and a major gain in CE would most likely occur from a more intense pest management program.

The average seed efficiency value of 0.376 is considerably below expected value for well-protected seed orchards. In the 1978 cones, 72.5 percent of the potential ovules failed to develop a filled seed. First-year aborted ovules were the major type of seed losses, with an average of 54.06 per cone. These losses could be from insufficient pollen or from insect damage. Of the two possible causes, insect damage by the leaffooted pine seedbug (Leptoglossus corculus (Say) appears to be the most likely cause of ovule mortality (DeBarr and Ebel 1973). Once the ovules enlarged in the second year of development, ovule abortion continued at a lower rate (average 4.95 per ovule). After seedcoat formation and fertilization, embryo mortality produces an empty seed. Causes of empty seed include insect damage, fungi, embryonic lethal alleles, and perhaps environmental stress. The total number of empty seed per cone was 22.65 and account for 31.0 percent of the total developed seed per cone. To increase seed efficiency, better insect control would appear to be the highest priority. If insects are adequately controlled, SE values should approach 0.65 to 0.75.

The average extraction efficiency of 0.833 for the sample cones is lower than the 0.90+ considered normal for the species. Unfortunately laboratory extraction may not accurately simulate operational orchard extraction. Thus the observed EE value for this orchard should be verified by extractions from the operational orchard extractory. Low EE values could be caused by early harvesting of cones and improper opening and extraction. For southern pines, seed extractories with recent innovations normally recover a high percentage of seeds from harvested cones.

Germination efficiency averaged 0.868 for the sample cones. This value is somewhat lower than normal for loblolly pine. No apparent cause of the lower GE value was evident. Normal values are 0.90 to 0.95 for loblolly orchard seed.

The overall seed orchard-to-nursery efficiency of 0.186 indicates that only 18.6 percent of the potential seed crop was recovered as viable seed for the nursery. Conversely, 81.4 percent of the potential seed crop was lost to numerous destructive causes. Based on the monitoring values, seed production of the orchard could be increased by reducing losses and subsequently raising the SO-NE value. The most obvious change in management strategy would be to increase the intensity of insect protection. Several major insect pests can be controlled with an integrated pest management program (DeBarr 1981). Further monitoring would then be required to compare the effectiveness of the pest management program in terms of a higher SO-NE value. The other approach to increase the orchard seed yields would be to increase the total female flower production. Cultural practices including fertilization, subsoiling, and thinning could be used to stimulate increased flower production. Even planting more acres of orchard is an alternative. The most cost-effective procedure, however, would be to evaluate the current management program and to continue monitoring annual seed and cone crops to measure the effectiveness and efficiency of the seed orchard management program.

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EFFECT OF NITROGEN FERTILIZER AND GIRDLING ON CONE AND SEED PRODUCTION OF WESTERN LARCH

Russell T. Graham

ABSTRACT: Western larch (Larix occidentalis Nutt.) is a poor cone and seed producer throughout northern Idaho. Because the species is important commercially, techniques for increasing seed production for both artificial and natural regeneration are needed. A study was conducted with western larch trees to evaluate the effectiveness of fertilizing, girdling, and a combination of fertilizing and girdling, as a means of increasing seed production. Girdling dominant and codominant 70-year-old western larch at the base of the live crown was very effective in stimulating cone production; the application of ammonium nitrate fertilizer in combination with girdling did not increase seed yield. Fertilizer alone did not increase cone production; rather, it appeared to decrease the number of seeds per cone. Cones from trees fertilized, girdled, and both fertilized and girdled had heavier seeds than cones produced by untreated trees.

INTRODUCTION

Western larch (Larix occidentalis Nutt.) is an infrequent and sporadic cone producer throughout northern Idaho. Since 1970, inventories of western larch seed for northern Idaho forests have been inadequate to meet needs of artificial regeneration programs. Because western larch is an important commercial tree species and the demand for seed exceeds the supply, a method of increasing seed production is needed.

Thinning forest stands has been shown to increase cone production in conifers. Wenger (1954) and Bilan (1960) showed that thinning increased cone production in loblolly pine (Pinus taeda L.), and Barnes (1969) found up to a fourfold increase in female strobilus production caused by thinning western white pine (Pinus monticola Dougl.). Barnes (1969) also found tree spacings of 9-m (29.5 ft) to be more effective than 6-m (19.7-ft) spacings for stimulating production of female strobili.

Mineral nutrition may also directly influence cone production of conifers. Nitrogen appears to be the most important element in cone production. Coast Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco.) (Ebell 1962, 1971), western white pine (Barnes 1969), and Rocky Mountain ponderosa pine (Pinus ponderosa var. scopulorum Engelm.) (Heidmann 1984) increased cone production in response to applications of nitrogen fertilizer. In addition, the type and timing of fertilizer application can be very important for cone initiation. Ebell (1972) found calcium nitrate fertilizer superior to urea and ammonium sulfate fertilizers in stimulating Douglas-fir cone production. He also found that application of fertilizer after 5 percent of the vegetative buds had burst in May stimulated cone production better than early spring or late spring applications. Fertilization rates of 225 kg per ha (201 lb per acre) of nitrogen to 1 800 kg per ha (1,607 lb per acre) of nitrogen have been found effective in increasing cone production of conifers.

Girdling is an effective method of increasing cone yields in some conifers. Bilan (1960) showed an increase in cone production attributable to girdling loblolly pine. Also, Ebell (1971) found a 300 percent to 400 percent increase in the number of cones on stems of Douglas-fir girdled at breast height compared to untreated stems. Holst (1959) reported a twentyfold increase in the number of cones produced on red pine (Pinus resinosa Ait.) because of girdling. He also found girdling trees at the base of the live crown was four times as effective as girdling at breast height for stimulating cone initiation. Stephens (1964) girdled individual branches of eastern white pine (Pinus strobus L.) and found 300 percent more female cones on the girdled branches than on the untreated branches.

Most girdles to stimulate cone production on conifers have been overlapping cuts up to one internode apart severing the phloem on two sides of the trunk or branch. They range from single saw cuts to complete removal of the bark. Girdling at breast height by removing a 2.5-cm (1-inch) strip of bark slightly more than half the stem circumference with an overlapping strip on the opposite side, one internode above the first, was used successfully by Ebell (1971) to increase the number of cones on Douglas-fir.

The purpose of this study was to examine the effects of girdling and fertilization,

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individually and combined, as a means of increasing seed production of western larch. Reported here are the results of such a combination of treatments on cone and seed production in a young western larch stand in northern Idaho.

METHODS

In 1980, we selected for this study a 70-year-old stand of western larch located on the Wallace Ranger District, Idaho Panhandle National Forests, 8 km (5 mi) east of Mullan, ID, near the Idaho-Montana border. The stand was thinned to a residual basal area of 9.2 to 13.8 m^2 per ha (40 to 60 ft^2 per acre). Logging slash was machine piled and burned in the spring and early fall of 1981.

Because snow cover prevented applying fertilizer in the spring before bud burst, the study was established in the fall of 1981. The treatments could then influence bud formation during the 1982 growing season. Seventy-two dominant and codominant trees were chosen in the stand and divided into six-tree groups. Only the best formed and more vigorous trees were chosen for inclusion in the study. Three treatments were randomly applied to six-tree groups in three replicates. The treatments included:

1. Fertilize: 336 kg per ha (300 lb per acre) of N in the form of ammonium nitrate was broadcast with a hand spreader under the crown of each tree, all within the drip line. This resulted in fertilizing a 4.5-m (14.8-ft) radius around the base of each tree.

2. Girdle: The trees chosen for girdling were climbed (using climbing spurs) to the base of the live crown. Here, a hand pruning saw was used to sever the phloem for one-half the circumference. A similar cut was made on the opposite side at least the length of the circumference down the tree. This resulted in overlapping cuts.

3. Girdle and fertilize: Trees were girdled and fertilized using the same procedures as for treatments 1 and 2.

Eighteen trees were maintained as controls, with no treatment. The treatment strategy resulted in a randomized complete block experiment with subsampling (table 1).

In the fall of 1983 each tree producing cones was climbed, and the cones were collected. Seeds were extracted from the cones and cleaned at the Coeur d'Alene Nursery at Coeur d'Alene, ID. Cones per tree, sound seeds per cone, and mean seed weight were recorded. In addition, a germination trial was conducted on the seed with 0, 14, and 28 days of stratification. An analysis of variance for a randomized complete block design was used to analyze the data (table 1). Duncan's multiple range test was used to detect differences among the treatment means.

Table 1.--Analysis of variance table for a study of effects of girdling and fertilization on cone and seed production of western larch in northern Idaho

	Analysis of variance	
Source	Degrees of freedom	Expected mean squares
3 Treatments and control	3	$\sigma^2 + 6\sigma^2_\varepsilon + 18\sum\tau^2_i/3$
3 Blocks	2	$\sigma^2 + 6\sigma^2_\varepsilon + 24\sum\beta^2_i/2$
Experimental error	6	$\sigma^2 + 6\sigma^2_\varepsilon$
Sampling error	60	σ^2
Total	71	

RESULTS

Girdling was highly successful in stimulating cone production on western larch. Trees that were only girdled had a mean of 832 cones per tree, the untreated trees had a mean of 77 cones per tree, the fertilized trees had a mean of 87 cones per tree, and the girdled and fertilized trees had a mean of 16 cones per tree (fig. 1). There were no significant ($P \leq 0.05$) differences in mean cones per tree among the fertilized, control, and the combination treatments, but the mean for the girdled treatment was significantly higher than the other means. Saw cuts on the girdled trees healed over within 1 year.

The only treatment that influenced the number of seeds per cone was fertilization. This treatment appeared to decrease the number of seeds per cone with a mean of only 0.63 (fig. 2); the control and other treatments all produced from 7 to 8 seeds per cone. The mean number of seeds per cone for the fertilized treatment was significantly lower than the means for the other treatments.

The treatments applied to stimulate cone production also affected seed weight. Seeds produced on the control trees were significantly lighter (3.11 mg) than seeds produced on treated trees (fig. 3). The heaviest seeds were produced on trees fertilized only, with a mean seed weight of 4.59 mg.

Other tree and site variables were tested to see if they had a significant relationship to cone production. Tree height, diameter at breast height (d.b.h.), crown ratio, crown density, and surrounding basal area were all tested to see if they were significantly related to cone production in addition to the treatments. The only variable close to being significant was crown ratio at the 0.163 level (table 2).

Tree height, crown density, d.b.h., and residual basal area were all nonsignificant in explaining the variation of cone production in western larch. In addition, there were few significant differences found among the treatments for the tree and stand characteristics (table 2). There were no differences in germination among the treatments after stratification of 0, 14, or 28 days. Germination means were 12, 95, and 96 percent, respectively, for the different stratification periods.

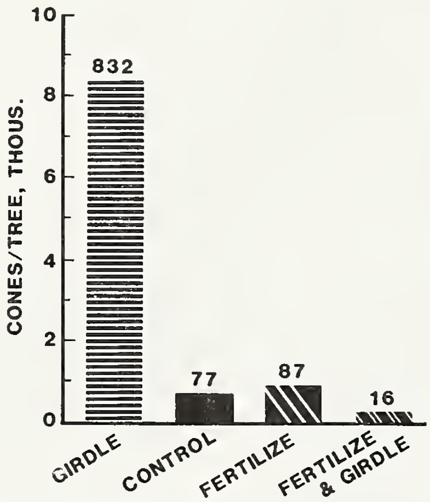

Figure 1.--Mean cones per tree produced by western larch after girdling, fertilization, and both treatments and by controls. The mean for cones after girdling was significantly higher than control and other treatment means. Differences among treatment means were not significant ($P \leq 0.05$).

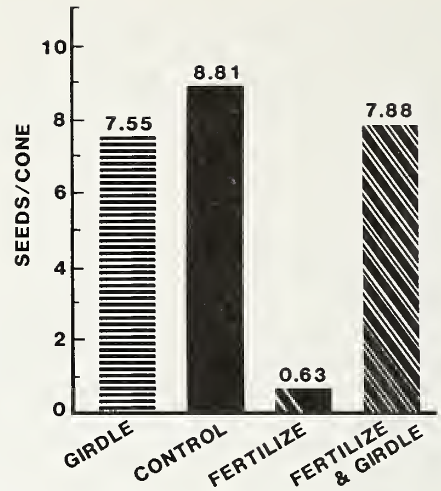

Figure 2.--Mean numbers of seeds per cone from western larch after girdling, fertilization, and both treatments and from controls. Fertilization apparently decreased the seed mean significantly. Other differences among means were not significant ($P \leq 0.05$).

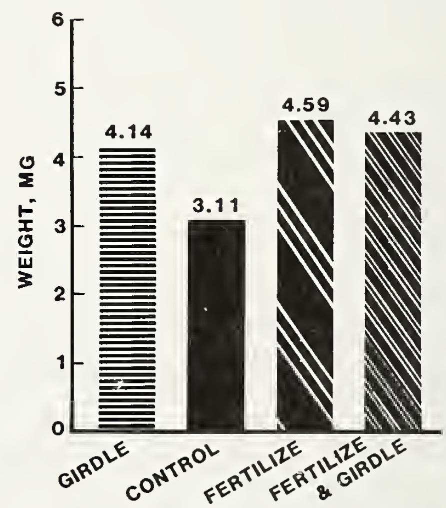

Figure 3.--Mean weights of seed produced by western larch after girdling, fertilization, and both treatments and by controls. The difference between the control mean and other means was significant ($P \leq 0.05$).

Table 2.--Mean tree and stand characteristics for western larch in northern Idaho by treatment and their significance in explaining cone production

Treatment	d.b.h.	Height	Crown ratio	Residual basal area	Crown density
	cm	m	percent	m^2/ha	
Control	[1]34.0a	28.9ab	31.7ab	8.66a	Good
Fertilize	35.3a	29.6a	35.0a	8.43a	Good
Girdle	33.5a	27.5bc	31.7ab	7.90a	Good
Fertilize and girdle	32.8a	27.0c	29.4b	6.89a	Good
Significance	.752	.367	.163	.752	.583

[1]Different letters indicate significant ($P \leq 0.05$) differences among treatments.

DISCUSSION

Girdling of western larch to increase cone production appears to be an effective method for use in seed production areas and for natural regeneration. Trees that were girdled produced more cones than trees that were fertilized only or both fertilized and girdled. Number of seeds per cone and mean seed weight appeared unaffected by girdling, and girdle cuts were healed within 1 year.

The application of 336 kg of N per ha (300 lb per acre) in the form of ammonium nitrate seemed to offset the stimulus to cone production caused by tree girdling. The addition of nitrogen may have increased tree vigor to the point that new growth consumed the increased nutrients but diluted any changes in hormones that may have occurred. The addition of nitrogen appeared to influence seed weight, but not to a greater extent than girdling alone.

The sawcuts apparently disrupted the translocation of organic solutes in the phloem enough to stimulate cone production. When the downward movement of organic solutes is blocked, they tend to diffuse into the xylem and are translocated back to the leaves and shoots of the crown (Kramer and Kozlowski 1979). These solutes containing carbohydrates, auxins, gibberlins, and other compounds can concentrate in leaves for fruit and seed production.

The accumulation of carbohydrates in the crown may not be directly associated with seed and cone formation. Ebell (1971) did not find an increase in the level of carbohydrates in the crowns of Douglas-fir that had been successfully girdled to increase cone production. He concluded that there was a doubtful relationship between carbohydrates and reproductive bud survival.

Besides disrupting translocation in the phloem, other physical conditions within a tree may be altered by girdling. These include increased moisture stress in tree crowns and changes in other physiological and nutritional processes that may increase cone and seed yields. In addition, the wound caused by a girdle may produce wound response compounds that could be redirected toward the crown to influence cone production.

Girdling trees at the base of the live crown appears very effective in stimulating cone production. The redirected movement of carbohydrates and hormones caused by girdling may be less diluted with girdles near the crown than with girdles at or near breast height. If there is a beneficial chemical response to the girdling wounds, this would also be near the cone-producing area of the tree.

Overlapping cuts through the bark at the base of the live crown created by a handsaw increased the number of cones produced on open grown western larch trees. Sawcuts healed after 1 year, making it possible to re-treat the trees relatively quickly with minimal permanent damage. However, climbing trees is time-consuming, and therefore expensive, and spurs often cause extensive damage. Therefore, with such good success by girdling at breast height in other species and the excellent results of this study, girdling at breast height should also be considered. Girdling trees at breast height may require more extensive bark removal to sufficiently disrupt translocation in the phloem. Heavier applications of fertilizer, in the range of 1,000 to 2,500 kg per ha (893 to 2,232 lb per acre) of N, might also be effective in stimulating cone production and should be investigated.

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FLOWERING OF PINACEAE FAMILY CONIFERS WITH GIBBERELLIN $A_{4/7}$ MIXTURE: HOW TO ACCOMPLISH IT, MECHANISMS AND INTEGRATION WITH EARLY PROGENY TESTING

Richard P. Pharis and Stephen D. Ross

ABSTRACT: Factors influencing the successful use of $GA_{4/7}$ to promote early and enhanced flowering in Pinaceae family conifers are reviewed, including the mode and timing of application, together with interactions with other growth regulators and cultural practices. Prospects for evaluating the inherent growth potential of progeny at a very young age under phytotron conditions and integration with indoor-potted breeding orchards to accelerate the tree-breeding process are discussed.

INTRODUCTION

It has been known since the late 1950s that juvenility could be terminated (albeit temporarily) and precocious flowering induced at will in seedling members of many Cupressaceae and Taxodiaceae family conifers through the exogenous application of gibberellins (GAs) (see ref. in Pharis and Kuo 1977). The potential usefulness of this treatment for accelerating the excruciatingly slow processes of breeding and production of genetically improved tree seeds was, of course, immediately recognized. It appeared for many years, however, that this effectiveness of GAs for promoting earlier and enhanced flowering in the Cupressaceae and Taxodiaceae did not extend to Pinaceae family conifers, which includes most of the commercially important species for which tree improvement programs were under way.

Then, in 1973, we discovered with Pseudotsuga menziesii (Mirb.) Franco (Pharis 1976; Ross and Pharis 1973) and later with other species (references cited in: Pharis and King 1985; Pharis and Kuo 1977; Pharis and Ross 1984; Ross and others 1983; table 1); that the GA in common use, GA_3, was the wrong one for using with the Pinaceae. Whereas GA_3 was especially effective with conifers of the Cupressaceae and Taxodiaceae, Pinaceae family conifers were found to exhibit a specificity for certain GAs less polar than GA_3, most notably a mixture of GA_4 and GA_7 ($GA_{4/7}$) (Pharis and Ross 1984; Ross and others 1983; table 1). In the past decade over 80 research reports have noted a positive flowering response to $GA_{4/7}$ for at least 18 Pinaceae species representing 5 of the 6 genera of this important family (table 1). The genus Abies is not included in this list but it has only been represented by a single study with A. homolepsis which gave equivocal results (Katsuta 1981).

The successful promotion of flowering is not, however, just simply a matter of spraying trees with $GA_{4/7}$. For reasons not yet understood (Pharis and Ross 1986) conifers of the Pinaceae are not nearly as responsive to applied GAs ($GA_{4/7}$) as are those of the Cupressaceae and Taxodiaceae (to GA_3). In this paper we will consider those factors and conditions which if met should ensure the successful promotion of early and enhanced flowering in Pinaceae family conifers using $GA_{4/7}$.

FACTORS INFLUENCING $GA_{4/7}$ EFFICACY

Treatment Timing

As with other stimulation treatments, $GA_{4/7}$ is only effective if its application brackets the period of cone-bud differentiation for the species in question. Owens gives elsewhere in this proceedings the times when seed- and pollen-cone buds first become anatomically distinct from vegetative buds for a number of North American conifers. He notes, however, that these times are the latest that treatments could be expected to promote flowering. For maximum effectiveness the treatment should be applied 2 to 3 weeks earlier to influence the biochemical processes leading to anatomical differentiation of bud types.

A few words of caution regarding treatment timing are in order. Many workers make the mistake of relating treatments to calendar date rather than to stage of bud development. Depending on the year, genotype, site and associated environmental/cultural conditions, etc., bud phenology may vary by 2, 4 or more weeks in any given trial. Consequently, where $GA_{4/7}$ applications are timed to calendar date the treatment may be either too early or too late to influence cone bud differentiation (Ross 1985). Fortunately, it is not

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Table 1.--A checklist for species of Pinaceae family conifers that will flower in response to application of a mixture of the plant hormones, gibberellin $A_{4/7}$, with appropriate reference citations

Species	References
Larix leptolepis	(see ref. cited in Pharis and Ross 1984; Bonnet-Masimbert 1982)
L. decidua	(see ref. cited in Pharis and Ross 1984; Bonnet-Masimbert 1982)
Picea abies	(see ref. cited in Pharis and Kuo 1977; Pharis and Ross 1984; see also Chalupka and Giertych 1977; Dunberg 1979; Dunberg and Oden 1983b)
P. engelmannii	(Ross 1985)
P. glauca	(Cecich 1985; Marquard and Hanover 1984a; Marquard and Hanover 1984b; Pharis and Kuo 1977; Pharis and others 1985)
P. mariana	(Hall 1984)
P. sitchensis	(see ref. cited in Pharis and Ross 1984; see also Philipson 1981; Philipson 1983; Philipson 1985; Tompsett 1977)
Pinus banksiana	(see ref. cited in Pharis and Ross 1984; see also Cecich 1982; Cecich 1983)
P. caribaea	(Harrison 1985)
P. contorta	(see ref. cited in Pharis and Kuo 1977; Pharis and Ross 1984)
P. densiflora	(see ref. cited in Pharis and Kuo 1977; Pharis and Ross 1984; Katsuta 1981)
P. elliottii	(see ref. cited in Pharis and Kuo 1977; Pharis and Ross 1984 and see also Hare 1984)
P. palustris	(see ref. cited in Pharis and Ross 1984 and see also Hare 1984)
P. radiata	(see ref. cited in Pharis and Kuo 1977; Pharis and Ross 1984 and see also Ross and others 1984)
P. sylvestris	(see ref. cited in Pharis and Ross 1984 and see also Chalupka 1978; Chalupka 1984)
P. taeda	(see ref. cited in Pharis and Ross 1984 and also Hare 1984)
P. thunbergii	(see ref. cited in Pharis and Kuo 1977; Pharis and Ross 1984)
Pseudotsuga menziesii	(see ref. cited in Pharis and Kuo 1977; Pharis and Ross 1984; Pharis and Ross 1976; Pharis and others 1980; see also Owens and others 1985; Pharis 1976; Pharis 1978; Ross 1976; Ross 1977; Ross 1978; Ross 1979a; Ross 1979b; Ross 1979c; Ross 1983; Ross and Pharis 1973; Ross and others 1983; Ross and others 1985; Webber 1984; Webber and others 1985)
	(see ref. cited in Pharis and Ross 1984; see also Pollard and Portlock 1984)
Tsuga heterophylla	(Dunberg and Oden 1983; Pharis 1978; Pharis and King 1985; Pharis and Kuo 1977;
Useful Reviews	Pharis and others 1980; Pharis and Ross 1984; Pharis and Ross 1986; Ross and Pharis 1982; Ross and Pharis 1986; Ross and others 1983; Zeevaart 1983; Zimmerman and others 1985)

necessary to go through the laborious process of dissecting axillary buds and potentially reproductive terminal buds (in some species) to determine when they are at the proper developmental stage for treatment. Reproductive bud development is closely related to the seasonal pattern of shoot elongation (Owens, this proceedings).

For Pseudotsuga (Ross 1983) and Tsuga (Ross and others 1980) $GA_{4/7}$ treatment would begin in spring at about the time of vegetative bud burst, whereas for Picea (Marquard and Hanover 1984b) it should be delayed until the new shoot is about 75-85 percent elongated. For these and most other Pinaceae family conifers the difference in timing of seed- and pollen-cone buds is generally too small to be able to use treatment timing to influence conebud sexuality (Owens, this proceedings). However, this is not the case for some species of Pinus, where it is possible to preferentially promote either male or female flowering through, respectively, early and late applications of $GA_{4/7}$ (Chalupka 1984). Another point to consider is that all buds on a tree do not develop at the same rate; in larger trees there will be much greater variation in bud development associated with crown position. Thus, whereas 2 weeks or less of $GA_{4/7}$ application may suffice to sexually differentiate a given bud (Owens, this proceedings), a longer treatment time is required to bracket the differentiation for different buds throughout the entire tree crown. The duration of treatment will also depend on the population of trees being treated and the magnitude of differences in their bud phenology. For most seed orchard populations it appears that 4 to 6 weeks of $GA_{4/7}$ application is about optimal for P. menziesii.

Mode of Application

Gibberellin $A_{4/7}$ costs about $13 to $20 (Can.) per gram, depending on source, so it is important that the mode of application be both effective and conserving of the hormone, as well as practical for operational use. The best mode of application will depend on the species, the size of the trees being treated and whether the objective

is to promote early and enhanced flowering for breeding purposes or for volume seed production. Thus, topical applications of $GA_{4/7}$ by micro pipette may be highly cost effective for the former but not the latter.

Foliar sprays are perhaps the most convenient method for applying $GA_{4/7}$ to large seed orchard trees. And, aqueous sprays containing an appropriate cationic surfactant have proved to be highly effective for certain conifers such as Tsuga heterophylla (Raf.) Sarg. (Ross and others 1980). However, for other conifers, including Pseudotsuga menziesii (Pharis and Ross 1976) and Larix species (Bonnet-Masimbert 1982), such foliar-applied $GA_{4/7}$ seems to be only poorly absorbed. Another problem with conventional foliar sprays is that they are quite wasteful of the $GA_{4/7}$. Ultra low volume (ULV) sprayers combined with anti-evaporant spray oils, which also facilitate foliar absorption, may provide a partial solution to both problems. Bower and Ross (1986) provide preliminary results which demonstrate its potential effectiveness for the operational $GA_{4/7}$ treatment of P. menziesii seed orchards. In this particular study, ULV spray applications in 2-percent spray oil elicited nearly three times the female flowering response at only 1/8 the dosage of $GA_{4/7}$ as the conventional aqueous surfactant formulation applied by high-volume mist sprayer.

Still for many conifers stem injection remains the most effective method for applying GAs (Pharis and Ross 1976; Bonnet-Masimbert 1982). As originally developed for Pseudotsuga menziesii, this involved feeding an aqueous solution of 25 to 100 mg L^{-1} $GA_{4/7}$ from a modified medical intravenous unit into a small (5/16-inch) hole drilled into the stem at the base of the live crown. Despite its effectiveness, the method was laborious -- injection holes plugged up after about 2 weeks and had to be redrilled -- and really only practical for treating relatively small trees. Philipson (1985) however, recently described a simpler method of stem injection which he found to be both quite convenient and highly effective for promoting flowering in large (6-m tall) Picea sitchensis (Bong.) Carr. trees. It involved drilling two shallow holes on opposite sides of the stem and then injecting with a syringe a concentrated ethanolic solution of $GA_{4/7}$. New holes were drilled after 2 weeks and the treatment repeated. Ross and Bower (1985, unpublished) are presently evaluating this quick method of stem injection (about 2 min/tree) on 4- to 14-cm diameter P. menziesii grafted propagules.

Interactions with Other Regulators

The less polar GAs are the only growth regulators that consistently promote flowering in Pinaceae family conifers (Pharis and King 1985; Pharis and Ross 1984; Pharis and Ross 1986; Ross and Pharis 1986).

The auxin, napthaleneacetic acid (NAA), was found by Hashizume (1967) to be an effective promoter by itself of female flowering in girdled Larix leptolepis saplings, but this was not the case for P. menziesii (Ross, unpublished results) or two species of Picea (Tompsett 1977; Dunberg and others, unpublished results). However, for these latter species NAA and other synthetic auxins were found to enhance the efficacy of applied GAs. In the case of sexually mature grafts of Picea sitchensis (Thompsett 1977) and in immature P. menziesii seedlings where the auxin was used at a higher concentration (Pharis and others 1980) the effect of applying NAA in conjunction with GAs was to promote male flowering at the expense of female flowering. However, with younger seedlings (table 2) and grafts (Ross 1976) of P. menziesii, synthetic auxins also enhanced the female flowering response to applied $GA_{4/7}$ although not to the same extent as for male flowering.

Table 2.--Female and male flowering responses by potted Pseudotsuga menziesii trees to stem injections of gibberellin $A_{4/7}$ ($GA_{4/7}$) alone and with the synthetic auxins, napthaleneacetic acid (NAA) or 2,4,5-triphenoxypropionic acid (2,4,5-TP) (Ross, unpublished results, 1979)[1,2]

Treatment	Cone buds/tree (no. ± s.e.) Female	Male
Untreated	12 ± 6	24 ± 14
$GA_{4/7}$ alone	67 ± 15	50 ± 17
$GA_{4/7}$ + NAA	78 ± 14	133 ± 45
$GA_{4/7}$ + 2,4,5-TP	100 ± 18	138 ± 38

[1]Plants were 5-year-old rooted cuttings of physiological age 12-14 years at time of treatment; 20 plants/treatment and grown outdoors in 17 L containers.

[2]Growth regulators were infused into the main stem, $GA_{4/7}$ at 100 mg L^{-1} and each auxin at 5 mg L^{-1} in 0.02 percent ethanol:water, for 12 weeks commencing approximately 2 weeks prior to vegetative bud burst.

On the other hand, studies with Tsuga heterophylla (Ross and others, unpublished results) and Pinus radiata D. Don (G. B. Sweet, personal communications) have found no response to NAA, either by itself or with $GA_{4/7}$ or GA_3. It seems that further research is required to establish if auxins and possible other growth regulators interact with GAs to influence cone-bud sexuality in conifers as is clearly the case for many angiospermous plants (Pharis and King 1985).

Interactions with Cultural Treatments in the Field

Promotion of flowering under field conditions is a tricky business, especially where young trees are involved. No single treatment, including $GA_{4/7}$ should be expected to work if site and climatic factors are otherwise unfavorable for flowering, as frequently appears to be the case in many of our seed orchards. However, many studies have shown that the probability of success is greatest where $GA_{4/7}$ is applied in conjunction with a cultural treatment (for example, nondestructive stem girdling, nitrate fertilization, rootpruning, or drought) that by itself is often ineffective in promoting flowering.

Table 3.--Interaction between gibberellins $A_{4/7}$+ A_3 and stem girdling on flowering in 7-year-old *Pseudotsuga menziesii* grafts at the Weyerhaeuser Company, Rochester, WA, seed orchard (Cade and others, unpublished results, 1975)[1]

Treatment	Clones Producing		Cone buds/tree	
	Females (percent)	Males (percent)	Seed (no.)	Pollen (no.)
Untreated	24 a	26 a	2.2 a	62 a
Girdled only	35 a	40 b	1.7 a	27 a
$GA_{4/7}$ + GA_3 only	67 b	30 a	7.8 b	20 a
$GA_{4/7}$ + GA_3 + gird.	97 c	74 b	50.7 c	337 b

[1]Values followed by the same letter do not differ significantly at $P \leq 0.05$ based on Chi square (percentages) and Duncan's multiple range tests.

[2]Trees received double overlapping, half-circumferential band girdles, 6 mm wide and 130 mm apart, at onset of vegetative bud swelling.

[3]Stem injections of a 1:1 (w/w) mixture of $GA_{4/7}$ and GA_3 in 0.02 percent ethanol:water also commenced then and continued for 9 weeks, during which time each tree received on average 1.13 g of the GA mixture.

[4]Each treatment was tested on 1-7 (3.8 avg.) ramets from each of 56 sexually mature parent tree clones.

Table 3 provides a classic example of such synergism, in this case between stem injections of $GA_{4/7}$ + GA_3 and overlapping band girdles in a 7-year-old grafted *P. menziesii* seed orchard in western Washington. Wheeler and others (1985) have shown that the same girdling treatment can be highly effective in the promotion of flowering for similar aged grafts in another orchard in southern Oregon. However, the Washington orchard was located on a relatively cool, moist site that was generally not favorable for early flowering, and here stem girdling by itself was totally ineffective in increasing the production of seed- or pollen-cone buds. The grafts responded with a small (though significant) increase in female flowering from stem injections of $GA_{4/7}$ + GA_3 alone. Yet, when combined, the hormone and girdling treatments had a highly synergistic effect, increasing the mean production of seed- and pollen-cone cones relative to the otherwise best treatment by factors of 5.6 and 44, respectively. Ross and others (1980) report a similar synergism between $GA_{4/7}$ and calcium nitrate fertilization for field-grown rooted cuttings of mature *Tsuga heterophylla* clones.

It should not be concluded from the above that $GA_{4/7}$ is always the most effective treatment. There are examples for *P. menziesii* where girdling (Bower and Ross 1986) and root-pruning (Ross and others 1985) were each more effective in promoting flowering than $GA_{4/7}$ alone. However, the point we wish to make is that best results have always been attained where the cultural treatment was applied in conjunction with the $GA_{4/7}$. What is furthermore important is that the magnitude of the synergism tends to be proportionately stronger for those inherently recalcitrant clones and families that without treatment might not contribute to seed production (Ross and others 1980; Ross and others 1985).

Benefits of Container Culture

The fact remains that, even with the best treatments, flowering under field conditions will still be subject to the vagaries of climate. Ross and others discuss elsewhere in this proceedings the practical advantages of managing small trees indoors in pots for seed production, central among which is the ability to provide optimal environmental conditions at the proper time for influencing cone-bud differentiation.

With *P. menziesii*, simply restricting the root volume of trees in small pots can by itself be sufficient to cause precocious or enhanced flowering. In one experiment grafts were either outplanted into the seed orchard in the spring of their second growing season or left outdoors in 2.1 L containers where they were kept well watered, with and without stem injections of 25 mg L^{-1} $GA_{4/7}$ for 6 weeks commencing at vegetative bud burst. The following spring only 14 percent of the outplanted grafts, but 80 percent of the potted but otherwise untreated grafts, initiated seed-cone buds, an average of 1.1 and 10.1 each, respectively. Treatment with $GA_{4/7}$ nearly trebled the production of seed-cone buds (to 28.1) by potted grafts and resulted in 94 percent of the grafts flowering.

A second experiment with 2-year-old rooted cuttings of P. menziesii seedlings only 2 years of age at time of propagation illustrates the importance of container size on flowering. Trees were repotted from 2.1 L into 6.3 , 19.7 or 76 L containers in early spring and received stem injections of $GA_{4/7}$ as above plus a heavy dosage of calcium nitrate. All trees were well watered and the following spring those in the smallest containers produced an average of 14.8 seed-cone buds each, compared to only 3.0 and 0.8 for trees in the 19.7 and 76 L containers, respectively.

Table 4.--Interaction between gibberellin $A_{4/7}$ ($GA_{4/7}$), water stress (WS) and stem girdling on female flowering in young potted Pseudotsuga menziesii trees (Ross, unpublished results, 1976)[1,2,3]

Treatment	Plants flowering (percent)	Seed-cone buds/tree (no.)
Untreated	5[a]	0.1[a]
$GA_{4/7}$ alone	50[b]	6.5[b]
$GA_{4/7}$ + WS[4]	60[b]	19.1[c]
$GA_{4/7}$ + gird.[5]	55[b]	13.5[c]
$GA_{4/7}$ + WS[4]+ gird.[5]	65[b]	7.0[b]

[1]Plants were 2-year-old rooted cuttings of physiological age 4 years from seed at time of treatment: 20 plants/treatment.

[2]Values followed by the same letter do not differ significantly at $P \leq 0.05$ based on Chi-square (percentages) and Duncan's multiple range tests.

[3]Stem injections of $GA_{4/7}$ at 25 mg L^{-1} in 0.05 percent ethanol:water began on 21 April and lasted 12 weeks.

[4]Throughout the period of GA treatment water stressed plants were allowed to attain an average pre-sunrise shoot water potential of -1.5 Mpa before watering to saturation. Non-stressed plants were well watered.

[5]Girdled plants received double overlapping, half-circumferential band girdles, 4 mm wide and 20 mm apart, beneath the lowermost live branch on 20 April.

It is not clear to what extent this reflects a more rapid build-up of favorable (to flowering) internal water deficits in the small containers, or reduction in root activity associated with pot binding (Bonnet-Masimbert 1982; Philipson 1983). Various studies on several conifers (table 4; Ross 1978; Brix and Portlock 1982; Bonnet-Masimbert 1982; Philipson 1983) have shown that drought produced by withholding irrigation frequently enhances synergistically the flowering response to applied $GA_{4/7}$ in potted trees. Note in table 4 that non-destructive stem girdling was nearly as effective in this regard as was drought, whereas the two cultural treatments applied together were apparently overly stressful and antagonized the flowering response to $GA_{4/7}$.

CONCLUSIONS

With Regard to Flowering

It appears to us, based on the plethora of successful reports noted in table 1 and in Pharis and Ross (1984), and the examples given in tables 2-4, that virtually any Pinaceae family conifer will be amenable to manipulation of early and/or enhanced flowering by the use of $GA_{4/7}$ + an appropriate cultural treatment. Additional gains in male flowering and increased female flowering may also be made through the judicious use of the auxin, NAA, given with the $GA_{4/7}$ and cultural treatment.

New species, and new or unusual climatic conditions (for field seed orchards) may require some additional empirical research with regard to optimal timing of treatment, dosages of hormone(s), and the most appropriate cultural treatment to use. In some locations climatic conditions (for example, wet cool, low solar insolation) may preclude successful field cone induction most years. In those cases, and perhaps in most instances, we recommend the use of potted propagules and heated plastic house environments during treatment (see paper by Ross and others, this proceedings).

In essence, there is now no excuse for a conifer tree breeder to wait for nature to bring on the 'natural' flowering that results from termination of the so-called 'juvenile phase'. All conifer species should be manipulable, even at very early ages, through the properly timed use of $GA_{4/7}$ application combined with an appropriate cultural treatment.

Additionally, enhanced production of seed from genetically superior propagules/F1 seedlings is now within our grasp (see Ross and others, this proceedings), and we believe that such an approach is, or can be, more cost effective than field seed orchards.

With Regard to Early Progeny Testing

Finally, we now have before us the very real possibility that inherently superior families, or even genotypes, can be tested at an early age (see table 5), and that young seedlings/germinants from these superior families and/or genotypes, can be multiplied clonally for outplanting. It is not unrealistic to visualize potted propagule seed orchards yielding, each

Table 5.--Effect of family and application of gibberellin $A_{4/7}$ mixture on the growth of *Pinus radiata* seedlings at different ages in the phytotron compared to growth rating of same families at age 9+ years in the field[a]

Family code[b]	Growth rating at age 9+ years in field[c]	Stem volume (cm^3) at ages[d] from germination: 138 days[e] Control (no $GA_{4/7}$)	175 days[f] Control (no $GA_{4/7}$)	175 days[f] $GA_{4/7}$-treated[g]	Stem volume increase due to $GA_{4/7}$ treatment (%)
R4	Fast	14.7(1)[h]	37.4(2)[h]	53.5(1)	43
R3	Fast	13.1(2)	36.2(3)	41.9(5)	16
R5	Fast	11.2(3)	39.4(1)	47.1(4)	20
R6	Fast	10.9(4)	29.5(7)	49.6(2)	67
R9	Slow	9.0(5)	29.8(6)	38.7(6)	30
R8	Fast	8.8(6)	27.8(8)	48.0(3)	73
R7	Slow	8.7(7)	34.4(4)	33.4(7)	-3
R2	Slow	8.7(7)	26.1(9)	32.4(8)	24
R1	Slow	8.3(8)	30.6(5)	27.1(9)	-11

Note: The effects of 'family' were evaluated statistically by ANOVA and the Duncan's Multiple Range test. Solid vertical bars connect family means which are not significantly different at $P \leq 0.05$. For $GA_{4/7}$-treated families vertical bars are not used, here R4 and R6 differed significantly from R1 at $P \leq 0.05$. Family R8 was 'bushy' (had a high proportion of d.w. in lateral branches) except for $GA_{4/7}$-treated plants, where volume (and also dry matter) was reallocated to the main stem. See also table 2 in Ross and others (1983) for an example of a similar reallocation in *Pseudotsuga menziesii*.

a Based on unpublished research results of R. Pharis, R. Griffin, K. Eldridge, M. Slee, G. Nikles, P. Cotterill.

b Seed was obtained from controlled pollination crosses made at least 10 years earlier, and was stored until germinated in November 1981. Parents are of New Zealand origin and were all classed as superior phenotypes ("plus trees").

c Field growth ratings of "fast grower" or "slow grower" were given to each family on the basis of volume and height growth at age 9+ over a wide range of progeny tests in southeastern Australia.

d Plants were raised in a phytotron at 25°C day/20°C night under natural daylength (November 1981 to May 1982); all plants received supplemental incandescent light for 16 hr/day in the phytotron.

e Stem volume was calculated from height and circumference (1 cm above cotyledons), averages based on measurements of 10 plants for each family (age 138 days).

f Stem volume was calculated from height and diameter (12 cm above cotyledons). Averages based on measurements of about three plants for each of control and $GA_{4/7}$ treatment groups, for each family.

g Gibberellin $A_{4/7}$ (about 55:45 GA_4:GA_7), obtained gratis from Imperial Chemical Industries, was applied as a root drench at 200 mg per L pH 8.0 (60 ml per pot, every 6 days from age 132 days) to three seedlings of each family. As part of the paired test, equivalent numbers of seedlings received H_2O as a "control" treatment.

h Values in parentheses represent family ranking within each test or age class.

year, several hundred thousand to several million 'superior' seeds. Each of those seeds from superior families could in turn yield 10 to perhaps several hundred vegetative propagules for out-planting. And, if the vegetative propagation is accomplished during the first year after germination, then loss of juvenile growth potential due to 'maturation effects' will be minimal or negligible. The following discussion, and table 5, discuss briefly the possibility of early progeny testing of families produced from F1 controlled crosses. Although we do not discuss it herein, a number of techniques exist to propagate young seedlings, including traditional and tissue culture techniques. Indeed, it now appears that somatic embryos of Picea abies, and perhaps Pseudotsuga menziesii, have been produced from juvenile tissue, and if somaclonal variability is not excessive, somatic embryogenesis may offer an alternative and highly effective means of clonal multiplication of superior families and/or genotypes. (Durzan, D.J. personal communication).

The possiblity that inherent vigour in vegetative growth may be 'testable' at a very early age is shown by data presented in table 5 for Pinus radiata. Early stem volume growth differed significantly between families by day 138 from germination (table 5), and if Δ stem volume growth [Ross and others (1983, table 4)] or stem d.w. is used, the significance of the differences is even more pronounced (data not shown). Similar tests on Pinus caribaea (Pharis and others, unpublished) and Picea mariana (Williams 1985; Williams and others 1985, unpublished) lead to the same conclusion -- there are strong and significant correlations between early growth in a Phytotron or glasshouse environment and growth in the field at about age 10 years.

Between age 138 and 175 days the P. radiata seedlings appeared to be getting 'pot-bound', and the attractive correlation between rank order in the phytotron and growth rating in the field is less strong (for example, compare control values at age 175 days with values at age 138 days -- Families R6 and R8 have dropped to rank order 7 and 8 respectively, and Families R7 and R1, both slow growers in the field, have risen in rank order to 4 and 5). However, for those plants which were treated with $GA_{4/7}$, Phytotron rank order still correlates very well with field growth rating (for example, the five fastest growing families in the phytotron are also fast growers in the field.

Hence, it appears that being 'pot-bound' may reduce stem volume growth (and other parameters also, data not shown) of some fast-growing families to a greater degree than slow-growing families. This lesion, however, appears to be 'cured' by application of $GA_{4/7}$ (table 5).

The $GA_{4/7}$ treatment causes an increased allocation of photo-assimilate to the main stem, often at the expense of the lateral branches for P. radiata (Pharis and others, unpublished) and Pseudotsuga menziesii (see table 2 in Ross and others 1983). Hence, families R6 and R8 may, under pot-bound or even normal conditions, have at least a modest deficit of endogenous GAs, or other mobilizing/growth factors. The 'other mobilizing/growth factors' may in turn be produced by or from endogenous GAs/exogenous GA application. The effect of $GA_{4/7}$ and/or high endogenous GAs could be as straightforward as providing more internodal volume in which to store photosynthate. Or GAs may have other or additional effects such as increasing ion uptake or 'mobilizing' photosynthate.

Thus, $GA_{4/7}$ application may be a useful additional tool to assist in discrimination between fast- and slow-growing families of P. radiata, and indeed $GA_{4/7}$ was also shown to be useful for this purpose with Picea mariana (Williams and others [1985], unpublished).

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POTENTIAL FOR CONTAINER SEED ORCHARDS

Stephen D. Ross, Andrea M. Eastham and Ralph C. Bower

ABSTRACT: Results are presented for Engelmann spruce and western hemlock which demonstrate the practical advantages of producing genetically improved seeds on small potted trees within a plastic-covered house. Relative to conventional soil-based orchards, these advantages include: earlier and more consistently abundant flowering; improved protection of cones and seeds; and strict control of pollen parentage, together with flexibility of clonal composition for maximum genetic gains. Because of more efficient space utilization and the greater ease and flexibility of management, production costs also promise to be lower.

INTRODUCTION

Potted trees, subject to strict control over environmental and treatment factors, have long been preferred by physiologists interested in studying the mechanism and control of flowering in conifers (e.g. Longman 1982; Ross 1985). Tree breeders, too, have occasionally capitalized on the relative ease with which precocious flowering can be induced, and controlled crosses subsequently made, using potted trees (Greenwood and others 1979). Until recently, however, there has been little serious interest in the management of small potted trees for volume production of genetically improved seed.

Since 1980, the British Columbia Ministry of Forests has been researching the development and evaluation of the indoor-potted seed orchards for western hemlock (Tsuga heterophylla (Raf.) Sarg.) and the interior spruces, Engelmann (Picea engelmannii Perry) and white (Picea glauca (Moench) Voss). With these species we faced (or would soon face) the same problems encountered with most conifers in attempting to produce genetically improved seeds in conventional soil-based orchards (Sweet and Krugman 1978; Ross and Pharis 1982). These included insufficient initiation of reproductive structures following a generally long "juvenile" phase; problems of pollination, including control of pollen parentage, and subsequent cone and seed development; and a host of management problems associated with tree size.

In this paper we review the potential advantages of indoor-potted seed orchards for more rapidly, completely and economically realizing the benefits of tree improvement. For convenience of discussion these are grouped into the three categories of production, genetic and management efficiency.

PRODUCTION EFFICIENCY

Initiation of Reproductive Structures

Many studies (Ross 1978, 1985; Tompsett and Fletcher 1979; Greenwood 1981; Bonnet-Masimbert and others 1982; Longman 1982; Philipson 1983) have demonstrated the relative ease with which potted trees can be induced to flower, given an appropriate stimulation treatment (see also Pharis and Ross in this volume). We illustrate this with two examples comparing, for western hemlock (table 1) and Engelmann spruce (table 2), the flowering response to induction treatments for potted and field-grown trees. Trees were vegetative propagules of mature plus-trees, with different clones and ramets of similar (spruce) or different (hemlock) ages, represented in the two orchard types. All treatment trees received spray applications of the growth regulator gibberellin $A_4/7$ ($GA_{4/7}$), calcium nitrate fertilizer and moderate drought (by withholding irrigation) appropriately timed for each species (Ross 1985; unpublished results). Potted trees of each species received these treatments both outdoors and in an unheated plastic-covered house (hemlock) or in a 30°C day:20°C night heated house (spruce). Heat treatment was also attempted for spruce in the soil-based orchard by enclosing grafts in a polyethylene tent.

Without treatment, flowering by both species in both orchards was rather poor. Treatment of western hemlock in the soil-based orchard increased from less than 5 to nearly 320 the mean number of seed-cone buds initiated per ramet, and from 27% to 100% the proportion of clones that flowered (table 1). However, the

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Table 1.--Comparison of 1985 flowering responses for 7-year-old potted and 12-year-old field-grown western hemlock rooted cuttings at the MacMillan Bloedel Harmac Tree Improvement Centre, B.C.[1,2]

	Potted seed orchard[1]			soil-based seed orchard	
	Untreated	Treated			
Flowering response	Outdoors	Outdoors	Indoors	untrt.	treated
Female flowering					
Ramets (=clones) Flowering (%)	75	100	100	27	100
Females/tree (no. ± s.e.)	52±22	257±65	427±63	3±2	319±131
Male flowering					
Ramets (=clones) FLowering (%)	56	73	86	36	61
Mean Pollen Score[3]	1	1.6	2.2	1	1

[1] All treated trees received calcium nitrate fertilizer in spring and 6 weekly foliar sprays of 200 mg L^{-1} $GA_{4/7}$ commencing at vegetative bud burst. Potted trees, additionally, were subjected to a simultaneous 6 weeks of moderate drought

[2] One ramet per clone per treatment, with a different group of 22-23 parent-tree clones represented each orchard

[3] Pollen cone production scored: 0 = none, 1 = light, 2 = moderate, 3 = heavy

Table 2.--Comparison of 1985 flowering responses to gibberellin $A_{4/7}$, drought and heat treatments for 7-year-old potted and 8-year-old field-grown Engelmann spruce grafted ramets representing different parent-tree clones (Ross, Birzins and Cox, unpublished results)

Flowering response	Potted orchard (Victoria,B.C.)			Soil-based orchard (Vernon, B.C.)		
	Outdoor	$GA_{4/7}$ + drought		Untrted	$GA_{4/7}$ + drought	
	Control	Outdoors	Indoors	Control	Alone	Tented
Ramets (clones)/trmt (no.)	16(16)	16(16)	16(16)	1489(296)	193(193)	410(209)
Female flowering						
Ramets producing (%)	12	69	75	10	17	24
Clones producing (%)	12	69	75	23	17	24
Cones/tree (no. ± s.e.)	1	30±9	54±33	1±1	2±1	11±4
Male flowering						
Ramets producing (%)	19	81	88	4	16	15
Clones producing (%)	19	81	88	19	16	23
Cones/tree (no. ± s.e.)	1	44±10	33±9	2±2	2±2	2±2

much younger (7 vs. 12 years) potted trees initiated in response to treatment indoors 33% more seed-cone buds each than the treated field-grown trees. Outdoors, the potted trees were less responsive to treatment, although here also 100% of the clones flowered.

The difference in treatment response was even more dramatic for Engelmann spruce where the grafts in the two orchards were of similar ages (table 2). As found by Chalupka and Giertych (1977) for Picea abies (L.) Karst., heat treatment by means of tenting significantly enhanced female flowering in the soil-based orchard, although still only 24% each of the ramets and clones produced seed-cone buds. In contrast, nearly 90% of the clones whose potted ramets received heat plus $GA_{4/7}$ treatment indoors flowered, and their mean production of seed-cone buds was almost four times that of the comparably treated field-grown trees.

As is typical for young soil-based orchards, pollen production here by both species was very sparse in relation to female flowering. In contrast, the smaller potted trees produced pollen in abundance. Furthermore, a significantly greater proportion of the clones contributed to this more profuse male flowering by potted trees, this again being particularly dramatic for interior spruce (table 2).

Where potted trees are properly managed (see below), there is no reason to assume that profuse flowering cannot be consistently achieved on a biennial basis. The potted trees in both studies reported here had flowered nearly as profusely in response to essentially the same treatments applied two years previously. This, however, was a first-time attempt at stimulation of the field-grown trees. Retreatment of a soil-based orchard may or may not be successful, depending on climatic conditions in the year of stimulation (Wheeler and others 1985). Adverse site and climatic factors can negate even the most effective of treatments, including applications of $GA_{4/7}$ in conjunction with nitrogen fertilizer, girdling and root-pruning (see Pharis and Ross in this volume).

High temperature and water stress generally appear to be the most important requirements for abundant flowering in many conifers (e.g. Pollard and Portlock 1981; Ross 1985). Their timing is also critical, as the results for Engelmann spruce in figure 1 clearly show. Cone-bud differentiation in this species is known to occur during the late stage of slow shoot elongation, and it is only at this time that heat treatment promotes flowering. Applied earlier, while shoots are rapidly elongating, its effect on flowering is strongly inhibitory, although water stress is highly promotive at that time and only then. This optimal sequence of early drought and late high temperatures seldom occurs in nature but is easily created in an indoor-potted orchard.

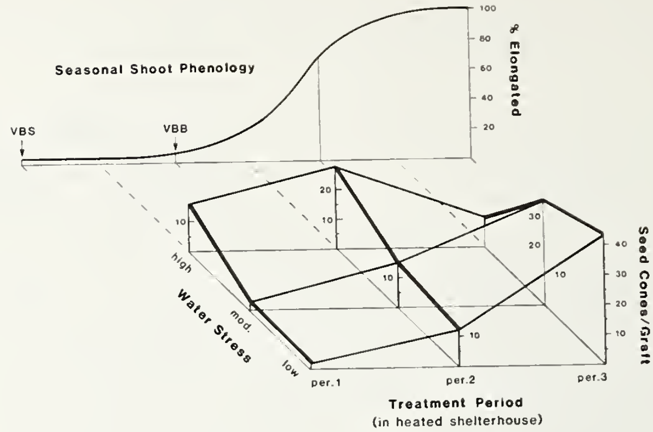

Figure 1.--Effect of heat and drought treatment timing on female flowering in young potted Engelmann spruce grafts. Ramets were moved into a 30° C day:20° C night heated shelterhouse at different stages of lateral shoot elongation (VBS and VBB refer to vegetative bud swelling and burst, respectively), during which they were either kept well watered or subjected to a moderate or severe drought by withholding irrigation until their midnight needle water potential had decreased to -0.75 or -1.5 MPa (adapted from Ross 1985).

Cone and Seed Efficiency

The ability to protect developing cones and seeds from adverse climatic conditions (high as well as low temperatures and wind) is another important advantage of indoor-potted orchards (see Bramlett in this volume). The ready accessibility of cones on small potted trees for inspection and spraying should also result in more effective insect and disease control.

Table 3 compares cone and seed traits for potted ramets of the same western hemlock clones that were induced to flower and subsequently maintained either outdoors or in a plastic-covered house without supplemental heat. Not only did the trees outdoors initiate significantly fewer seed cones, but the proportion of those that survived was also significantly lower than indoors. This was the result of several severe freezes during winter and early spring. Outdoors, the surviving cones contained fewer total (filled plus empty) seeds as well, probably for the same reason. Possibly the different conditions of heat and water stress under which trees were induced to flower indoors and outdoors the previous year had a carry-over effect on subsequent cone and seed development. However, our results suggest that so long as trees are not overly stressed during induction such carry-over effects are relatively small.

In a soil-based orchard, especially a young one, pollen is likely to be limiting for good seed set (see tables 1 and 2). This was not a

Table 3.--Cone and seed traits compared for potted western hemlock rooted cuttings induced and maintained outdoors or in an unheated greenhouse (Eastham and Ross, unpublished data)[1,2]

Trait	Outdoor ($\bar{X}$+s.e.)	Indoor ($\bar{X}$+s.e.)
Cones initiated/tree (no.)	320±23	633±30
Surviving cones/tree (no.)	198±13	529±26
Cone efficiency (%)	62	84
Total seed/cone (no.)	27±1	31±1
Filled seed/cone (no.)	10±1	14±1
Seed efficiency (%)	37	45
100-filled seed wt. (mg)	200±5	199±5
28-day germination (%)	79±5	82 ±5

[1] Rooted cuttings were 7-years old at time of induction, with 3-8 ramets each of the same 8 plus tree clones

[2] See footnote 1 of table 1 for description of induction treatment.

consideration in the present comparison of indoor and outdoor potted trees (table 3). Unbagged female strobili on both groups of trees were supplementally pollinated at least three times when maximally receptive with the same pollen lot (from potted ramets indoors). Even then, however, the filled seed percentage was significantly lower outdoors. Cool, moist conditions prevailed outdoors throughout the pollination period and this could have adversely affected pollen germination and subsequent fertilization of ovules.

Potted trees in this study were maintained in the plastic-covered house following pollination. However, this does not appear to be necessary, or in the case of some species, particularly desirable for good subsequent cone and seed development. Where flowering Engelmann spruce grafts were subject to elevated temperatures within an unheated house, the resulting cones were significantly smaller relative to ramets whose cones matured outdoors (Ross, in prep.). These cones also contained significantly fewer total seed, of which a smaller percentage was filled.

For this species, and presumably most conifers, optimal conditions for cone and seed development are the same as those that favor vigorous vegetative growth-- that is, abundant water and nutrients along with moderate temperatures. These are not the conditions that promote flowering. Another advantage of working with potted trees, therefore, is that they may be managed separately for each initiation and subsequent development of reproduction structures to ensure maximum production of high quality seed. This is not generally possible in a soil-based orchard.

GENETIC EFFICIENCY

Control of Pollen Parentage

It is no secret that the wind-pollinated orchard is not very efficient when it comes to capturing the genetic benefits from tree improvement (Sweet and Krugman 1978; Smith and Adams 1983; El-Kassaby and others 1984). Dilution of genetic gains from contaminating foreign pollen is a serious problem in many such orchards. Where orchards are located off site, the seed produced may also be maladapted to the planting region. Furthermore, only a relatively small proportion of the orchard parents may be contributing male and female gametes. Of these an even smaller proportion may have the opportunity to mate due to the nonsynchrony in timing of pollen shedding and female receptivity among clones. The situation is thus ripe for selfing and other departures from truly panmictic mating, with potentially deleterious effects on realized genetic gains.

Indoor-potted orchards, on the other hand, allow a degree of control over pollen parentage not feasible in conventional wind-pollinated orchards to achieve maximum-possible genetic gains. The approach to pollen management will depend to a large extent on the status of the breeding and testing program.

Artificial pollination may not be warranted when dealing with untested clones. But even then positive steps can be taken to ensure more nearly panmictic mating. At the very least, the potted trees can be effectively isolated indoors from foreign pollen. And, it may be expected that a larger proportion of clones will be contributing male and female gametes than in the soil-based orchard (tables 1 and 2), which should reduce the potential for self pollination. Reproductive bud development in spring can be synchronized, either hastened or slowed as required for late- and early flushing clones, respectively, by moving their potted ramets into a warmer or cooler house.

It is, however, where information on the mating value of individual orchard clones is available that the genetic benefits from pollen management in indoor-potted orchards will be greatest. This may involve supplemental mass pollination using pollen collected from the very best parents. Even more attractive is the opportunity to mass produce progeny of elite full-sib families through controlled crossing, and thus capitalize on that portion of the nonadditive genetic variance associated with specific-combining effects.

Unlike the problems encountered with large trees in soil-based orchards (see Sweet and Krugman 1978), artificial pollination is relatively easy with small potted trees. Certain clones (and even ramets within clones) have a tendency to initiate mainly seed cones or pollen cones, and these may be managed separately as female and male parents. In

early spring the female parents might be moved outdoors to slow their reproductive bud development relative to pollen parents left in an unheated house. This will ensure the necessary lead time for collection and processing of pollen from all clones prior to the onset of female receptivity (J.E. Webber, pers. com.). The pollen is easily harvested, either by picking individual pollen cones as they mature, or shaking the tree and collecting the shed pollen on a sheet of paper. We have found the latter method to be particularly convenient for species, such as western hemlock, which have very small pollen cones. The female parents are then moved back indoors for artificial pollination at the optimal time with high viability, fresh pollen.

Infusion of New Selections into Production

By the time a conventional orchard comes into full production, 10 to 15 or more years after establishment, its seed may already be genetically obsolete. Even if progeny test results are not available before then, most orchards will have already required a silvicultural thinning by that age. The opportunity to use these results to rogue inferior clones from the orchard therefore may be limited as well. With an indoor-potted orchard the lag time between selection and seed production for new clones is considerably shorter. Also, unlike conventional orchards, whose clonal composition is determined at time of establishment, the potted orchard may be continually upgraded genetically as new selections become available. It is not only more efficient genetically, but far less expensive as well to replace individual potted ramets than an entire soil-based orchard.

We call this in situ advancing-front, and the concept of orchard generations no longer applies (Ross and Pharis 1982). In the case of a new tree improvement program, the potted orchard would probably contain ramets of all plus-trees in sufficient number to meet projected seed requirements over, say, the next 10 years. Breeding and seed production could occur simultaneously, but with primary emphasis given initially to the former so as to minimize delays in progeny test establishment. Progressively more severe roguing of inferior clones would then occur over time as the progeny tests become older and their results more reliable. Initial roguing of parents could perhaps begin on the basis of four year or younger progeny test results, with selection among progeny of the best families occurring several years later (Lambeth 1980; Pharis and Ross in this volume). The clones thus eliminated might be replaced initially by extra ramets of the proven parent clones (as required for seed production), but ultimately by ramets of new advanced-generation selections. Even then, the potted orchard could still contain some highly superior parents from previous generation(s).

MANAGEMENT EFFICIENCY

Production Costs

Indoor-potted orchards may be more efficient than soil-based orchards in terms of providing earlier production of seed of higher genetic quality, but we are frequently asked are they practical and cost effective? We are only just beginning to acquire comparative cost-benefit data for the two types of orchards, but for western hemlock and interior spruce the answer does appear to be yes.

Consider the hypothetical case of two interior spruce orchards, one potted and the other soil based, each with a production capacity of five million viable seeds per year. Using Birzin's (this volume) expected yield of 4,000 viable seeds per ramet per annum by age 15 years after grafting, and a final spacing of 5m x 5m (1250 ramets rogued from an initial 2500), the soil-based orchard would occupy nearly 3.5 ha, exclusive of roads and support facilities. Our results indicate that each interior spruce ramet in an indoor-potted orchard is capable of producing on average 3,000 viable seeds every other year beginning at age 7 years in response to biennial induction treatment. Thus, a potted orchard with the same five-million annual production capacity would contain about 3,300 ramets but only occupy 700m^2 of covered houses and a like area of outdoor container yards. (Only half the ramets would be indoors at any one time-- for cone induction and pollination-- except possibly for freeze protection over winter when they can be tightly packed to conserve space.)

Even a very superficial analysis indicates that the potted orchard will probably be less costly to establish. One does not require a sophisticated controlled-environment greenhouse -- a plastic-covered house with propane heater and let-down sidewalls for natural ventilation will suffice. In this example, the cost to construct two such houses (10m x 35m) and a 700 m^2 outdoor container yard, each equipped with movable pallets and automated drip-irrigation system, should not exceed $45,000 (costs in 1985 Canadian dollars). Assume another $8,000 to propagate the additional 800 ramets which the potted orchard requires (3300 vs. 2500 initially for the soil-based orchard).

However, the potted orchard requires little space. It can be sited anywhere, on relatively inexpensive and otherwise nonproductive land-- perhaps in conjunction with a container nursery where certain facilities and equipment can be shared. On the other hand, proper site selection is crucial to the success of the soil-based orchard (Birzins, this volume). And, sites conducive to abundant flowering tend to be in short supply and high demand for agricultural use. Such land in the Okanagan Valley of interior B.C. currently goes for about $17,000 per hectare (Birzins, pers. comm.), for a total purchase price of nearly

$60,000 for the 3.5 ha orchard in this example. That does not include site preparation, road construction, fencing or irrigation systems.

The indoor-potted orchard is equally attractive from the standpoint of potentially lower operating costs. Contrary to popular belief, container culture for seed production need not be highly labor intensive. Much of the work (potting and plant handling, irrigation and applications of fertilizers, pesticides and GAs) can be automated to a large degree. There are the additional expenses for pots, media and heating, but these promise to be small in relation to the large amounts of fertilizers and other chemicals and water used in soil-based orchards. Finally, there are large economies to be realized in the induction, pollination, protection and harvesting of cones when working with small, potted trees.

In comparing the two orchards one must also consider the difference in time and value of seed produced. There are two costs associated with the longer nonproductive phase of the soil-based orchard (15 vs. 7 years for the potted orchard in this example). There is the time-discount factor and the opportunity cost of delayed realization of genetic benefits. In this example, the indoor-potted orchard could already have produced 40 million viable seed by the time the soil-based orchard came into commercial production. That relates to approximately 16,000 extra hectares of new interior spruce plantations containing the very best possible genetically improved trees.

Production Flexibility

Indoor-potted orchards offer a unique flexibility of management. Their production capacity can be rapidly scaled upwards or downwards in response to changing seed requirements. The mobility of potted trees also allows for most efficient site utilization. Unlike soil-based orchards with their fixed-tree arrangement, the potted orchard can start off small, and then be expanded as needed to accommodate the increasing size of trees.

Another advantage of indoor-potted orchards relates to a point made by Libby (1985). He notes that "Seed-orchards are sensitive to economies of scale, and one can rarely justify a seed-orchard for local low volume demand." Even with so-called 'major' species having a large total annual seed requirement, this production is often divided among many breeding zones each represented by its own small orchard. Several of these may be consolidated on a single site for increased management efficiency, but then there is the possibility that seed will be maladapted to their site of utilization due to cross-pollen contamination between the different breeding zones. Trees from many breeding zones may be managed as a single group in a potted orchard, except when separated for pollen management.

In a potted orchard one can also conceive of utilizing controlled pollinations to capitalize on those unique characteristics of individual clones (such as disease or drought resistance or special wood properties), of the same or different breeding programs, to custom produce progeny that are specifically adapted to certain problem sites or for minor, but valuable end products.

Finally, potted orchards are also most attractive for those minor species whose annual seed requirements hardly justify a seed-orchard program, but which are poor seed producers in nature. Chamaecyparis nootkensis (D. Don) Spach, a species not widely planted but still highly prized for its quality wood, is an excellent example. In containers this species flowers profusely at a very young age in response to GA_3 treatment (Bower, unpub. data). A desirable strategy for such a species might be to rapidly build up a number of years' supply of seed in a small orchard, and then discard the potted ramets which could easily be repropagated when the seed supply again runs low.

CONCLUSIONS

Compared to conventional orchards, indoor-potted orchards offer the potential for attaining earlier, more reliable seed production and maximum-possible genetic gains through sexual reproduction, all with a much greater efficiency of management. The biological feasibility of producing genetically improved seed on small, potted trees is now well established for many conifers. And, further research will lead to improved efficiencies of production and management. However, for western hemlock and the interior spruces this research has progressed to the point where we are now ready to begin pilot testing the approach for cost effectiveness on a semi-operational scale.

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MANAGING BLACK SPRUCE SEEDLING SEED ORCHARDS FOR CONE AND SEED PRODUCTION

Ronald F. Smith

ABSTRACT: The use of fertilizers to stimulate cone production in black spruce (Picea mariana (Mill.) B.S.P.) seedling seed orchards is discussed. The types, rates, and time of fertilizer application are reviewed, with emphasis on the causes of inconsistencies in responses to fertilizer treatments. The interactions between initial tree spacing and the time and degree of rogueing and tree response to fertilizing are briefly reviewed.

INTRODUCTION

In New Brunswick, seedling seed orchards are established on 'typical' planting sites. Although seedling orchards are not managed as intensively as clonal orchards, cultural practices such as fertilizing to enhance cone production will be necessary for these orchards to be fully productive.

Applying fertilizer is the most common technique currently employed for enhancing cone production in seed orchards. However, no one type of fertilizer or rate of application has been successful in all instances (Sweet and Hong 1978). The effectiveness of any fertilizer treatment in enhancing cone production varies with tree size, tree spacing, the type of fertilizer used, the rate, method, and timing of application, the weather immediately following fertilizer application, and the genetic predisposition of the trees to produce cones.

Fertilizer and spacing experiments were established in 8-to 10-year old black spruce (Picea mariana (Mill.) B.S.P.) plantations from 1980-1982 (Smith 1983). This paper summarizes some of the factors that influenced the effectiveness of applying fertilizers to enhance cone production and discusses the results as they apply to managing seedling seed orchards.

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FACTORS AFFECTING RESPONSE TO FERTILIZING

Tree Size

Female and male cone production were positively correlated with both tree height and diameter, but the correlations were higher for diameter (Smith 1983). Small trees did not respond as well to fertilizer treatments as did large trees (fig. 1). In some instances, small trees did not respond at all to treatment regardless of the type or rate of fertilizer applied.

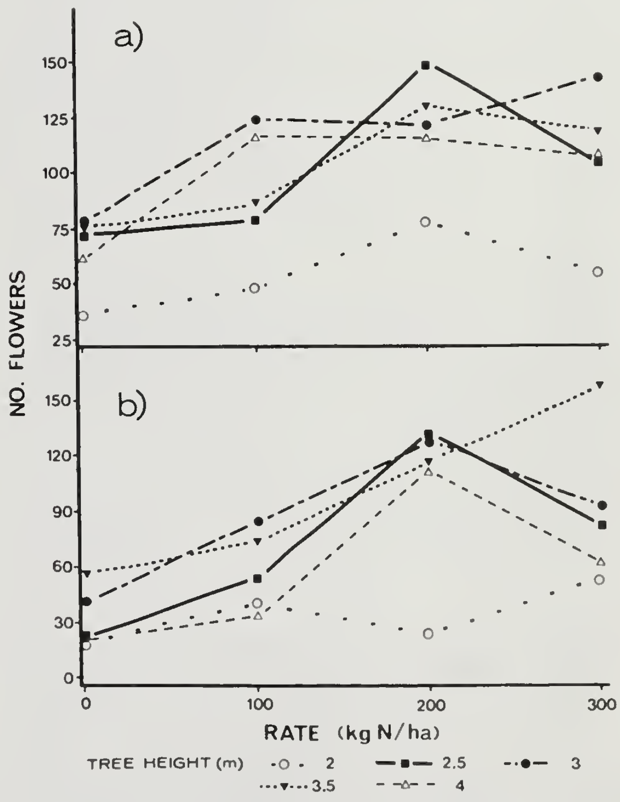

Figure 1. -- Relation between a) female and b) male cone production in black spruce (1982) and tree height and the amount of ammonium nitrate fertilizer applied in 1981 (May - June).

Tree Spacing

Tree spacing affects the capacity of seed orchard trees to respond to fertilizer treatments in that trees growing at wider spacings have fuller crowns with more potential flowering sites (greater numbers of buds). Fertilizing did not increase the number of buds, but rather the proportion of buds which developed reproductively (Smith 1985).

The degree to which spacing will limit response to fertilizing differs between species. In red pine, (Pinus resinosa Ait.) female cones can be borne on a large portion of the live crown. The number of cones per tree may increase with increased spacing until the total number of cones per unit area decreases due to the reduced number of trees (Stiell 1971). In young black spruce however, female cones were generally borne in only the top three or four whorls. The number of potential flowering sites in the upper crown limited the degree to which female cone production increased in response to wider spacings. However, trees at wider spacings did produce more cones of both sexes (fig. 2).

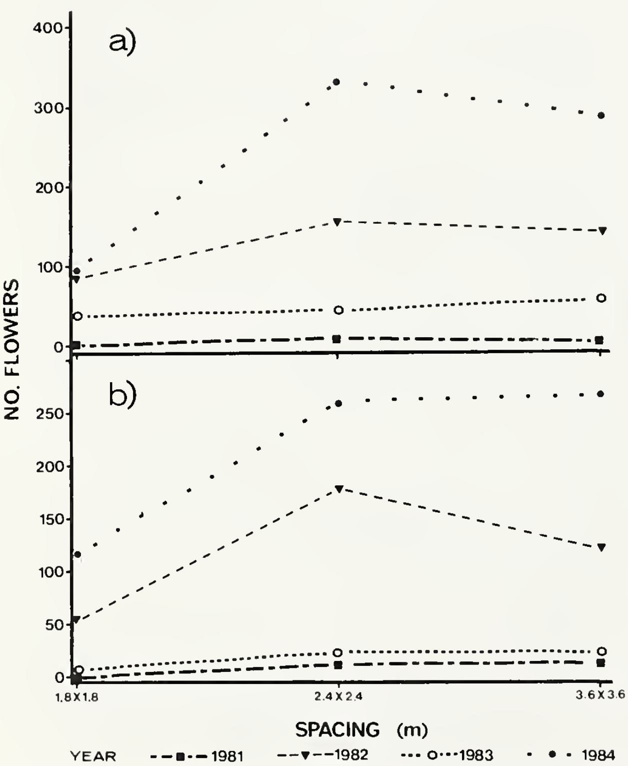

Figure 2. -- Effects of spacing on a) female and b) male cone production in black spruce.

Seedling seed orchards are often planted at close spacing, e.g., in New Brunswick, 1 X 2 m (3 X 6 ft) or 1.5 X 2 m (4.5 X 6 ft). Rogueing removes genetically 'inferior' families (trees) thus allowing the remaining trees to develop full, vigorous crowns capable of supporting large cone crops. However, growth rate of the trees affects the time and intensity of the rogueing, as trees must be removed before growth and, concomitantly, seed production within the orchard is affected. Orchards located on very fertile sites may require rogueing earlier and to a heavier degree than might be justified from the family test measurements alone.

Type of Fertilizer

Nitrogenous fertilizers, particularly those containing the nitrate (NO_3) form of nitrogen, e.g., ammonium nitrate and potassium nitrate, have been most successful in stimulating cone crops (Puritch 1977). Applying ammonium nitrate increased both male and female cone production in black spruce whereas applying urea did not (Smith 1983).

Rate of Application

The rate at which fertilizer is applied determines whether or not flowering will be affected, and if so, positively or negatively. Fertilizing black spruce at rates greater than 300 kg N/ha decreased both female and male cone production, but especially the latter (fig. 3). Both the amount of fertilizer required per tree to elicit the maximum cone production response, and the rate at which overfertilization occurs, increases with tree size (Ebell 1972a).

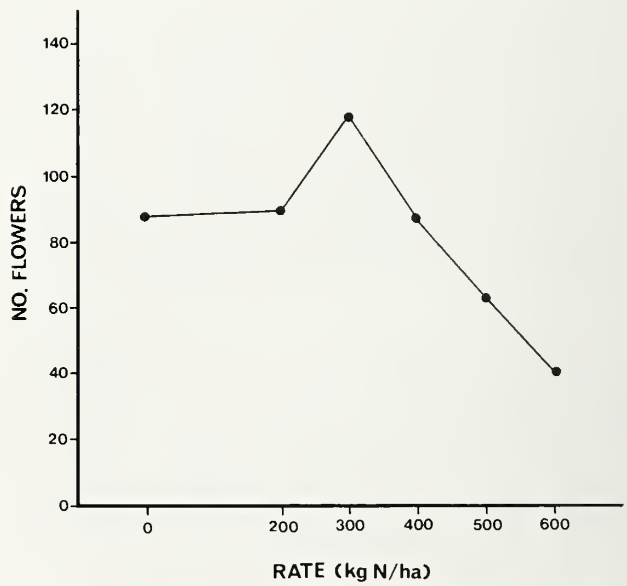

Figure 3. -- Relation between rate of ammonium nitrate fertilizer application and male cone production in 1982 for black spruce trees fertilized in 1980 (from Smith 1983).

Method of Application

The amount of fertilizer applied is usually expressed as the total amount of fertilizer or nutrient per unit area. However, the effectiveness of fertilization in stimulating cone produc-

tion is determined by how much of the applied fertilizer each tree receives. Fertilizer should be placed under the crown dripline because the bulk of a tree's root system lies within this area. Band-type spreaders are better than cyclone types because there is better control of fertilizer placement.

Broadcast applications are more effective for large than for small trees as their root systems occupy more of the site. If a broadcast method is used, more fertilizer per hectare may be needed to elicit a flowering response, i.e., the amount of fertilizer lost to uptake by other vegetation will be more than if the same total amount of fertilizer was applied, but placed in a band around each tree. When accessibility within the orchard precludes using broadcast methods, hand applications are necessary. Hand applications allow for rates to be increased for large, and decreased for small trees, respectively, which should optimize the flowering response.

Timing

The time that trees are fertilized will determine whether vegetative growth, reproductive growth, or both, will be affected. Fertilizer must be applied before the reproductive buds for the next year are formed (primordia differentiation). In Douglas-fir, April and May fertilizer applications significantly increased cone production whereas June applications did not (Ebell 1972b), because primordia differentiation in Douglas-fir occurs in late May to June (Owens 1969). Owens and Molder (1979) give growth and development patterns for the major North American genera. These general guidelines could be used by orchard managers to determine approximately when differentiation occurs, enabling them to establish approximate 'not-later-than' dates for fertilizer applications when the exact phenology for their species and orchard sites is not known.

In black spruce, applying fertilizers up to two months prior to the approximate time of primordia differentiation still significantly increased cone production the following year (Smith 1983). In southern pine orchards, fertilizer can be applied as much as one month earlier than the 'recommended' times for female cone induction (Schmidtling 1983) conferring the advantage of coordinating fertilizer applications to periods of reduced workloads.

Effects of Weather

Response to fertilizing is usually best when the weather conditions during the year of application are conducive to the initiation of strobili, e.g., the response year is a 'good' cone crop year. In black spruce, trees did not respond to fertilizing as well in naturally 'poor' flowering years as in 'good' years; only the larger trees showed an increase in cone production in these 'poor' years.

Weather influences the rate of fertilizer uptake and the total amount of nutrient which actually becomes available to the tree roots. Heavy rainfall immediately after applying fertilizer can cause a high proportion of the fertilizer to be leached through the soil. When this occurs, the cone-induction effect of the applied fertilizer can be lost. The cone-induction effect of fertilizing can also be lost under warm, dry conditions, i.e., fertilizer will deliquesce more slowly, perhaps remaining in the soil longer. When this occurs it also takes longer for the fertilizer to reach the root surfaces. If fertilizer is applied close to the time of primordia differentiation, the proportion of the fertilizer which actually reaches the roots in time to affect cone production could be reduced, thus reducing its effectiveness in stimulating flowering. When this occurs, the rate at which fertilizer should be applied to maximize cone production must be increased (Ebell 1972b).

Genetic Effects

Probably the most important factor influencing cone production in seed orchards is the genetic predisposition of the trees to flower. Differences between clones account for a large proportion of the total variation in flowering in seed orchards (Sprague and others 1979; Schmidtling 1983). Consequently, genetic effects can mask the effects of fertilizer treatments. Adding nitrogen can increase the numbers of flowers produced, but will generally not induce those trees to flower which were not 'predisposed' to do so (Robinson 1979; Barnes and Bengston 1968).

Genotype-fertilizer interactions at the family level have been reported for conifers (Jahromi and others 1976; Maliondo and Krause 1985). The effectiveness of fertilizer treatments in inducing cone production for different families is not well documented. The strong fertilizer-clone interactions in reponse to applying nitrogen fertilizers (Robinson 1979; Sweet and Krugman 1977) would indicate that family differences can be expected. It is, however, impractical on an operational scale to formulate fertilizer recommendations on a family basis. Consequently the fertilizer and rate which is effective for 'most' families should be used.

The only means of managing the genetic component within seedling seed orchards is through selecting which families or individuals are to be removed. Fecund individuals within the best families can be favored over nonbearing trees given that these trees also exhibit good growth characteristics. Similarly, trees which respond well to cone-induction treatments may be favored over those which do not respond well. Flowering records, by family, should be kept to evaluate accurately fecund families and trees within the orchard.

CONCLUSIONS

The following practices should be followed if the maximum benefit from applying nitrogen fertilizers to stimulate cone production in black spruce seedling seed orchards is to be realized.

1. Orchard rogueing must be scheduled such that tree spacing never limits crown development and, concomitantly, the capacity of the trees to respond to cone-induction treatments.
2. The type of fertilizer used, and the rate, method, and timing of application must be considered in planning fertilizer schedules.
3. Records of flowering in the orchard should be kept so that the final rogueings favor not only the best families (based on family test measurements), but also the more fecund trees within these best familes.

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245 VARIATION IN CONE AND SEED PRODUCTION FROM NATURAL STANDS, PLANTATIONS, AND CLONAL-BANKS OF LODGEPOLE PINE //

Cheng C. Ying and Keith Illingworth

ABSTRACT: Information reported in this paper is based on: 1) 780 parent trees from 53 provenances of the inland form of lodgepole pine (Pinus contorta ssp. latifolia); 2) a wind-pollinated progeny plantation of 778 families derived from (1), planted in 1973, and in which conelet production was recorded in 1979, 1980, and 1981 (age 10, 11, and 12 from seed); and 3) 160 clones (800 grafts) in two clone banks, which were planted in 1972, and in which conelet production was recorded annually since establishment. Both (2) and (3) are located at Red Rock, south of Prince George, British Columbia.

The results suggest that:

1. a managed clonal seed orchard can produce commercial quantities of seeds (over 200 cones per graft) in 10 years;
2. a clonal orchard may produce better quality seeds than natural stands (grafts produced 44% more seeds per cone and seeds 48% heavier than did natural stands);
3. large clonal variation in both seed- and pollen-cone production capability will not only affect the genetic composition of seed orchard seeds, but also the balance between maximizing genetic gain and maintaining seed production capacity at the time of seed orchard roguing;
4. differential cone production capability among provenances is inherited rather than environmentally induced, and that provenances of northern latitude origin are more precocious but less prolific than the southern latitude ones;
5. the current strategy of concentrating seed orchards for the central Interior at Red Rock and for the southern Interior at Vernon appears to be appropriate biologically and economically, in view of the strong geographic trend among provenances in cone production capability, particularly of pollen cones;
6. seed orchards for northern British Columbia and the Yukon probably should not be located south of latitude 56°N in view of their poor growth at many sites in the central and southern Interior British Columbia.

Paper presented at the Conifer Tree Seed in the Inland Mountain West Symposium, Missoula, MT, August 5-6, 1985.

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INTRODUCTION

This paper reports geographic and year to year variation in conelet production and seed yield of lodgepole pine in natural stands, in a wind-pollinated (w.p.) provenance-progeny test plantation, and in two clone banks, emphasizing their practical implications for seed orchard planning.

Lodgepole pine has become a major planting species in the Pacific Northwest. In the interior region of British Columbia alone, planting of lodgepole pine reached 15 million seedlings in 1983 (i.e., 20% of the total seedlings planted), and is projected to reach 73 million seedlings (40% of the Interior program) at the turn of the century. The goal of planting only genetically improved trees by the year 2000 (B.C. Ministry of Forests 1980) has led to the rapid expansion of a tree improvement and seed orchard program in the British Columbia Interior. Seed orchards are the most expensive phase of a tree improvement program and their efficiency determines, to a large extent, the cost-benefit ratio of such a program. Information reported in this paper provides a basis for improving the efficiency of lodgepole pine seed orchard planning in terms of their location, size, and projected seed yields.

SOURCE MATERIAL AND DATA COLLECTION

Cone production and seed yield data were gathered from three sources:

1. about 780 parent trees from 53 provenances of the inland form of lodgepole pine (Pinus contorta ssp. latifolia) (Critchfield 1980). The majority of the provenances comprised 15 parent trees. The number of seeds per cone and 1000-seed weight were determined for each parent tree;
2. a wind-pollinated progeny plantation of 778 families derived from (1). The plantation was established in 1973 with 2+1+1 stock, and was laid out according to a compact-family (split plot) design (provenance designated as main plot and family the sub-plot with three replications of 6-tree family plot). Spacing was 3.7 x 3.7 m. Seed- and pollen-cone production were recorded by counting the number of conelets and pollen clusters in the spring of 1979, 1980, and 1981 (age 10, 11, and 12 from seed) as follows:

	Number of		
Year	Prov.	W.P. fmlies	Trees
1979	53	778	8888 (in 2 reps)
1980	53	778	8835 (in 2 reps)
1981	10	148	828 (in 1 rep)

Various numbers of pollen clusters were sampled from many flowering trees to determine the average number of microstrobili per pollen cluster for each family and provenance.

3. one hundred and sixty clones (800 grafts) in two clone banks, named SCA and SK. Grafting was done in 1971 and 1972, and both clone banks were established in the fall of 1972 with five ramets per clone in a single row, spaced 3.7 x 3.7 m. The two clone banks were planted side by side. SCA contains clones from the north, and SK from the south, of latitude 56°N approximately (fig. 1), and 335 of the 375 grafts in SCA (75 clones) and 337 of the 425 grafts (83 clones) were living in 1985. Seed- and pollen-cone production were recorded every year since planting, and in 1981 seed yield and seed weight were determined for a sample of 20 clones representing their geographic distribution (Ying and others 1985b).

Both the w.p. progeny plantation and the clone banks are located at Red Rock (lat. 53° 46'N, long. 122° 42'W, elev. 580 m), south of Prince George. The climate at both sites is similar, but the soils are very different: the clone banks are located on a deep, freely drained silty sand, the progeny plantation is on a stony glaciofluvial terrace.

Geographic locations (fig. 1) of parent trees in (1) and (2) and ortets of 3) are summarized below:

Source	Lat.(N)	Long.(W)	Elev.(m)
(1 & 2)	49°04'-63°18'	114°25'-136°18'	455-1815
(3)	49°18'-63°22'	120°10'-136°17'	250-1478

Data were subjected to variance analyses, and correlation and multiple regression were employed to elucidate the relationship of cone production at different ages and with the geographic origin of provenances.

SEED YIELD AND SEED WEIGHT

Both seed yield (i.e., number of seeds per cone) and seed weight showed large variation from

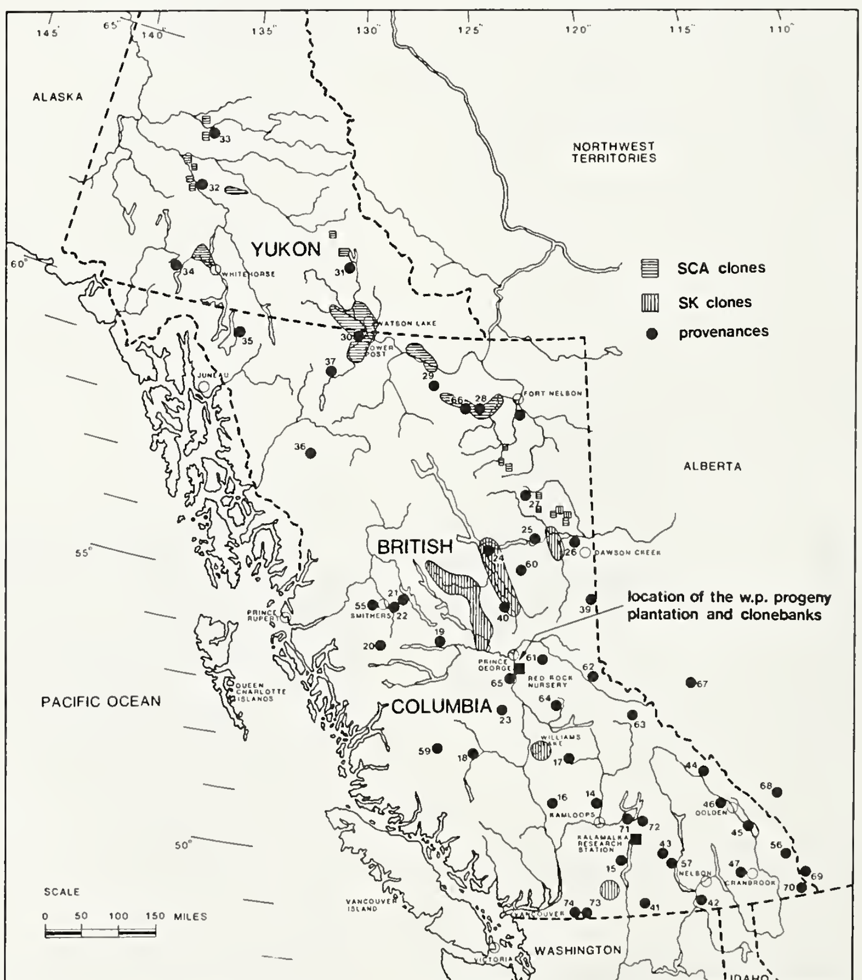

Figure 1.--Geographic origin of the 53 provenances and the ortets in SK and SCA clone banks.

Table 1.--Comparison in number of seeds per cone and 1000-seed weight between natural and grafted lodgepole pine

	No. seeds per cone		1000-seed weight (mg)	
Geographic region	Natural stands	Grafts	Natural stands	Grafts
Yukon and Northern B.C.	22	24	2.6	4.1
Southeastern B.C. and Alberta foothills	12		3.2	
Central and Southern B.C.	16	22	2.8	3.8
Coast-interior transition	11		2.5	
Mean	16	23	2.8	4.0
Range (provenance means)	9-31		2.2-3.9	
Range (tree or clone means)	1-64	5-39	1.4-4.6	3.3-4.9

provenance to provenance, tree to tree, or clone to clone (table 1). Variance analyses indicated 40% among- versus 60% within-stand variation. Grafts produced 44% more seeds per cone and these were 48% heavier than trees in natural stands (table 1).

Significant and positive correlations between number of seeds per cone and latitude and longitude (table 2) suggest a northwest-southeast geographic trend: trees from the Yukon Territory and northern British Columbia produced the highest number of seeds per cone, and those from Alberta, southeastern British Columbia, and near the coast-interior transition zone were among the lowest (table 1). An opposite geographic trend was evident in seed weight (table 2): trees from Alberta produced the heaviest seed and those from the Yukon and near the coast-interior transition, the lightest (table 1). However, the range of variation in seed weight was rather small (table 1). This confirms the conclusions of Birot (1978) and Critchfield (1980) that variation in seed weight is largely a character of the subspecies. Latitudinal and longitudinal trends were not as obvious in the clone banks probably due to the small number of clones (20) studied and the large within-provenance variation (Ying and others 1985b). Results from both the clone banks and natural stands indicated poor seed yield of high-elevation trees.

Table 2.-- Correlation of number of seeds per cone and 1000-seed weight of natural lodgepole pine trees with latitude, longitude and elevation of their origin (based on provenance means, n = 53)

	No. seed per cone	1000-seed weight
Latitude	.66 [a]	-.32 [b]
Longitude	.50 [a]	-.60 [a]
Elevation	-.38 [a]	.18

[a] Significant at 0.01 level.
[b] Significant at 0.05 level;

SEED- AND POLLEN-CONE PRODUCTION

Grafts

Seed- and pollen-cone production were recorded in the clone banks over a 12-year period (fig. 2); both seed- and pollen-cone production increased steadily after planting except for the unexpected decline in 1983. Most grafts produced a commercial quantity of cones (over 200 conelets per graft) 10 years after planting. Pollen-cone production, although about 5 years behind initially, reached the level of commercial quantities at about the same age as seed-cone production, and therefore would not affect the commercial production of a clonal seed orchard (fig. 2).

Grafts in the SCA clone bank (northern latitude origin) started to produce both seed and pollen cones earlier, but were eventually out-produced by those in the SK clone bank (southern origins) (fig. 3).

Seedlings

Seed- and pollen-cone production of the 10 provenances (148 families) counted in all 3 years (1979-81) are presented in table 3. Pollen-cone production showed a sharp increase from 1979 (age 10) to 1980 (age 11), and the increase from 1980 to 1981, though not as spectacular, was still substantial, with the exception of #31 from the Yukon. Average number of pollen clusters per living tree in 1981 was 25 times that in 1979 (table 3). Compared with pollen-cone production, changes in seed-cone production from 1979 to 1981 were relatively small: most provenances showed a moderate increase from 1979 to 1980, but decreased from 1980 to 1981 (table 3). The range of provenance difference in pollen-cone production was much larger than that for seed cones. For example, in 1981 the most prolific provenance produced almost 10 times more pollen cones than did the least prolific one, excluding the atypical provenance #31, but the ratio of difference

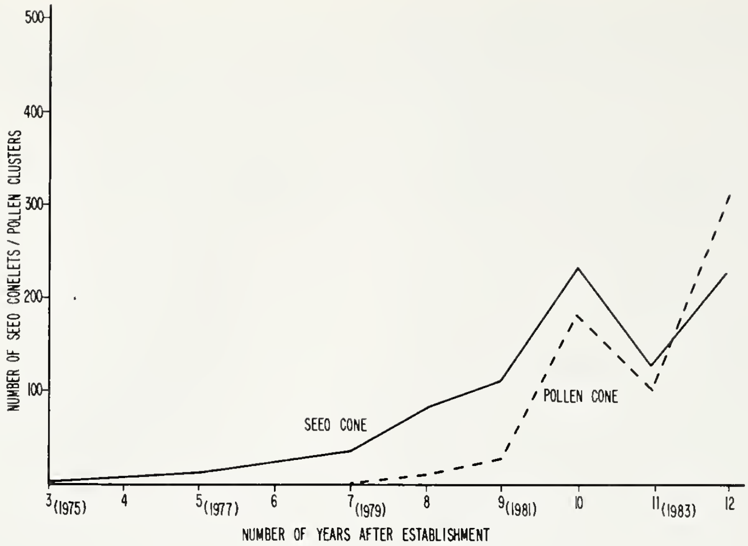

Figure 2.--Average yearly seed- and pollen-cone production in the two grafted clone banks.

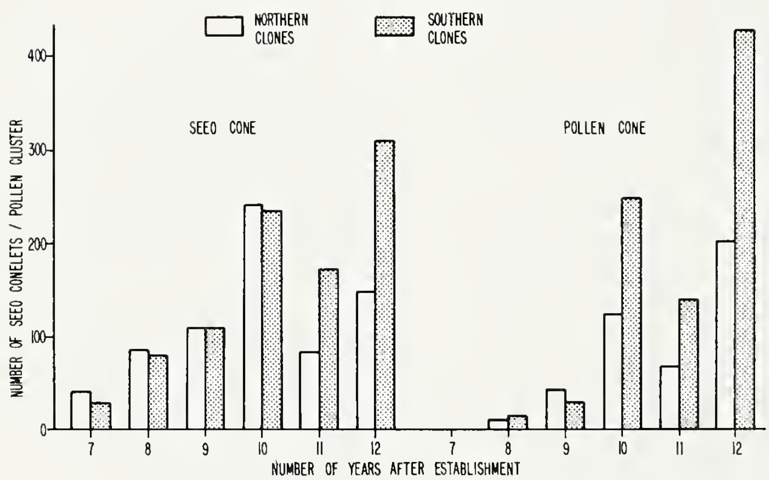

Figure 3.--Comparison in seed- and pollen-cone production between clones of northern latitude (SCA) and southern latitude (SK) origin.

between the most and the least productive provenances was only about 2 to 1 for seed-cone production (table 3). The change of the pollen cone - seed cone ratio from 0.9 at age 10 to 10.5 at age 12 (table 3) also reflected the differential pollen- and seed-cone production. Mean number of microstrobili per pollen cluster varied very little among provenances or from year to year (table 3).

Differences among provenances and among families within provenances were all statistically significant, but over 60% of the variation was associated with the tree-to-tree differences within w.p. families.

Grafts Versus Seedlings

Comparison in conelet production between the grafts in the clone banks and the seedlings in the w.p. progeny plantation is not, strictly speaking, valid because they were neither from the same geographic locations, nor planted at the same site in the same year, receiving the same cultural treatments. However, a comparison of mean production at different ages should be reasonably valid because the numbers of grafts and seedlings investigated were large and they were from similar geographic areas (fig. 1). This comparison is given in table 4. The grafts produced 5 to 10 times more seed cones than the seedlings, and showed similar superiority in pollen-cone production at age 10 and 11. At age 12, however, the seedlings produced as many pollen cones as the grafts. The percent of individuals bearing seed cones or pollen cones was higher in grafts in the clone banks than in seedlings in the w.p. progeny plantation, particularly in the earlier ages.

Table 3.-- Average number of seed cones and pollen clusters, their ratio, and average number of microstrobilus of the 10 provenances which were counted from 1979 (age 10) to 1981 (age 12), provenances arranged from north to south

Provenances					Seed cone			Pollen cluster			Pollen cluster /seed cone			Microstrobilus		
No.	Location	Lat.	Long	Elev (m)	10	11	12	10	11	12	10	11	12	10	11	12
31	Frances L., Yukon	61° 10'	129° 20'	884	18	26	3	0	1	2	0	0.1	1.2	19	20	17
66	Stone Mt., B.C.	58° 39'	124° 46'	1173	22	30	18	0	6	23	0	0.3	1.9	21	22	24
27	Pink Mt., B.C.	57° 00'	122° 24'	1113	23	30	32	1	16	53	0.1	0.8	2.3	29	21	26
60	Mt. Lemory, B.C.	55° 33'	122° 33'	732	13	29	27	2	22	82	0.3	1.1	7.0	25	30	27
63	Albreda, B.C.	52° 35'	119° 10'	975	14	46	36	11	114	170	1.8	2.7	12.8	31	28	30
17	Oie L., B.C.	52° 00'	121° 12'	991	10	21	21	6	35	181	1.7	2.9	22.1	27	27	31
14	Wentworth Cr., B.C.	50° 58'	120° 20'	1059	8	30	16	3	34	111	1.0	1.3	18.0	25	28	29
72	Larch Hills, B.C.	50° 42'	119° 11'	777	6	33	20	7	106	189	2.1	3.6	19.2	28	22	32
68	Kananaskis, Alta.	51° 01'	115° 02'	1501	12	26	22	4	55	112	0.7	2.6	6.8	28	28	27
45	Settlers Rd, B.C.	50° 31'	115° 44'	1036	28	82	39	13	199	254	0.8	3.1	11.3	27	32	35
	Mean				15	35	24	5	61	123	0.9	1.9	10.5	27	28	29
	LSD.05				6	10	8	6	36	39	1.8	1.5	8.2	8	4	6

Table 4.--Comparison in seed- and pollen-cone production between grafted and seedling lodgepole pines

	Seed cone bearing				Pollen cone bearing			
	Graft		Seedlings		Graft		Seedlings	
Age	%[a]	Mean[b]	%[a]	Mean[b]	%[a]	Mean[b]	%[a]	Mean[b]
10	98	113	84	15	68	28	21	5
11	100	237	96	35	89	185	62	61
12	99	128	90	24	80	103	78	123

[a] % of grafts or seedlings bearing seed or pollen cone.
[b] Mean number of conelet or pollen cluster.

Table 5.--Correlation coefficients of mean number of seed cones and pollen clusters, and pollen cluster - seed cone ratio with the latitude, longitude, and elevation of the provenance origin

	Seed cone			Pollen cluster			Ratio		
Origin/age	10	11	12	10	11	12	10	11	12
Latitude	.40	-.19	-.50	-.12	-.37	-.89	-.04	-.03	-.78
Longitude	.23	-.24	-.67	-.32	-.51	-.80	-.10	-.29	-.46
Elevation	-.21	-.19	.09	-.06	-.12	-.07	-.10	-.33	-.26

Notes: 1. Correlations were calculated from provenance means.
2. Age 10 and 11 data are based on 53 provenances; age 12 data are based on 10 provenances.
3. Correlation coefficients significant at 0.05 level are underlined.

Geographic Trend

Correlations of cone production with latitude and longitude of the provenances were relatively high in the w.p. progeny test (table 5). The correlation coefficient increased with the age of the trees for pollen-cone production, but changed from positive to negative for seed-cone production. This indicates that provenances from the northwest (i.e., the Yukon) were more precocious but less prolific than those from southeastern British Columbia (i.e., East Kootenay). A similar trend was also evident with the grafts (fig. 3).

Table 6.--Regression analyses with seed cone, pollen cluster, and pollen cluster - seed cone ratio as dependent variables and latitude, longitude and elevation of the provenance origin as independent variables using maximum R^2 method

Number of variables in model	Intercept	Latitude	Longitude	Elevation	R^2
			Seed cone		
One	226.6		-1.68[a]		.45
Two	300.9	1.64[N]	-3.02[N]		.52
Three	466.1	3.30[N]	-4.92[a]	-0.03[N]	.68
			Pollen cluster		
One	1130.9	-18.72[b]			.79
Two	1242.5	-19.35[b]		-0.07[N]	.83
Three	1976.7	-10.13[N]	-9.75[N]	-0.13[N]	.86
		Pollen cluster - seed cone ratio			
One	94.6	-1.56[b]			.61
Two	-69.3	-3.97[b]	2.43[b]		.95
Three	-63.1	-3.90[b]	2.34[b]	-0.00	.95

[N] The regression coefficient not significant.
[a] The regression coefficient significant at 0.05 level.
[b] The regression coefficient significant at 0.01 level.

Table 7.--Age/age correlation (r-value) in seed- and pollen-cone production, and their ratio (pollen cluster:seed cone) estimated by covariance analyses based on the 10 provenances counted from age 10 (1979) to 12 (1981) in w.p. progeny plantation

	Seed cone			Pollen cone			Ratio		
	Age pairs			Age pairs			Age pairs		
Source	10/11	10/12	11/12	10/11	10/12	11/12	10/11	10/12	11/12
Provenance	.62	.39	.66	.95	.92	.87	.85	.88	.74
Families/Prov.	.40	.48	.49	.68	.41	.62	.34	.32	.20
Trees/Fam./Prov.	.57	.46	.56	.56	.30	.53	.31	.17	.20

Regression analyses (table 6) of w.p. progenies revealed that latitude, longitude, and elevation of the provenances together accounted for 68, 86, and 95% of the observed variation for seed-cone production, pollen-cone production, and their ratio respectively, but the effect of elevation was not significant in any case. Geographic trends in seed- and pollen-cone production of grafts in the clone banks were not as obvious (Ying and others 1985b). This can be expected in view of the large within-provenance variation mentioned before.

Age/Age Correlation

High age/age correlation in cone production was observed for both seedlings (table 7) and grafts (table 8). This was true for provenance, family, and individual trees (table 7). These results suggest that a few precocious and prolific clones or seedlings could contribute a large proportion to the genetic composition of the seeds, particularly those harvested from the early years of a seed orchard (Jonsson and others 1976; O'Reilly and others 1982; Todhunter and Polk 1982).

Table 8.--Age/age correlation (r-value) in seed-cone and pollen-cone production based on clonal means. All correlation coefficients are significant at 0.05 level.

Year (age)	1980	1981	1982	1982
		Seed cone		
1979 (8)	.78	.48	.44	.33
1980 (9)		.71	.66	.52
1981 (10)			.68	.52
1982 (11)				.50
		Pollen cone		
1979 (8)	.46	.81	.41	.43
1980 (9)		.67	.51	.57
1981 (10)			.56	.54
1982 (11)				.80

Cone Production and Growth

Correlation between cone production and height growth were all positive at the level of provenance, family, and individual tree (table 9), indicating that tall trees were also heavy cone producers. In an earlier study, Lee found an invariable positive correlation between cone production and various growth characteristics in these two clone banks. There is no indication of negative effects of flowering on vegetative growth in either grafts or seedlings of lodgepole pine (Nilsson 1981).

Table 9.-- Correlation of total height at age 13 with seed-cone and pollen-cone production at age 12 in the w.p. progeny plantation, using covariance analysis technique

	Correlation between height and	
Source	Seed cone	Pollen cone
Provenances	.61	.86
Families/P	.11	.35
Trees/F/P	.15	.27

DISCUSSION AND IMPLICATIONS

The superiority of grafts in seed yield and seed weight (table 1) suggests that seeds from a clonal seed orchard will be of better quality than the seeds from natural stands, and thus should produce better quality seedlings and improve the nursery recovery factor (the ratio of number of plantable seedlings over number of seeds sown). The nursery recovery factor for seed from clonal seed orchards is predicted to be 0.6 as compared to 0.4 for seed from natural stands (Hewson and others 1984). The low seed-cone production by the seedlings (table 4) suggests that clonal orchards would be superior to seedling orchards in terms of seed yield. However, the lack of pollen-cone production by the grafts during the first 7-8 years (fig. 2) can hinder the rapid advance of a breeding program. Field observation indicated more balanced seed- and pollen-cone production by the seedlings at the early ages. Moreover, the response of grafts to cone-enhancement treatment in lodgepole pine has not been encouraging (Wheeler and others 1982).

It is interesting and useful to compare the seed- and pollen-cone production in the w.p. progeny plantation at Red Rock with that of a similar trial at Ange, Sweden (lat. 62° 32'N, long. 15°42'W, elev. 200 m), which contained provenances from similar geographic origins (Nilsson 1983):

Age (year)		Seed cone		Pollen cone	
Red Rock	Ange	Red Rock	Ange	Red Rock	Ange
10(1979)	15(1978)	15	8	5	26
11(1980)	16(1979)	25	10	61	35
12(1981)	17(1980)	24	13	123	45

Although the Ange plantation was 4 years older, the amount of cone production was only about half of that at Red Rock. Apparently, plantation location has a major impact on cone production.

The pattern of geographic variation observed at Red Rock was also very different from that at Ange: positive correlations between seed-cone production and latitude of the provenance origins were found at Ange (Nilsson 1981), but at Red Rock this correlation was positive only at age 10 (table 5). In other words, at Ange more northern provenances showed more abundant seed-cone production, and this pattern changed little from year to year. At Red Rock, however, this north-south pattern was observed only in 1979, and in 1981 provenances of southern latitude out-produced the northern ones (table 3). No geographic trend in pollen-cone production was apparent at Ange, but a declining northwest to southeast trend was obvious at Red Rock (tables 3, 5, and 6).

Differential adaptation among provenances to respective test sites is apparently the main reason for this disparity in the geographic variation pattern of cone production between Ange and Red Rock. Our experience indicates that vigorous vegetative growth is a prerequisite for abundant cone production in lodgepole pine (Wheeler and others 1982); high correlation between growth and cone production (table 9) suggests that vigorous trees produced more cones (Nilsson 1981). Trees of the Yukon and northern British Columbia seed sources grew poorly in the Red Rock plantation, and at most sites in Interior British Columbia, indicating their poor adaptation (Ying and others 1985a). This apparently also affected their cone production capacity. On the other hand, these northern provenances have been the major sources of lodgepole pine seeds for reforestation and were found to grow well at most sites in Sweden (Lindgren 1983). Poor cone production of the southern provenances at Ange was evidently related to their low vigor. These results suggest that the selection of seed orchard location should follow the similar general guidelines used for seed transfer (Ying and others 1985a, 1985b).

At Red Rock, the prolific cone production of seedlings and grafts originating from southern latitudes (fig. 3, table 3) does not seem to support the common belief that the southward transfer of seed orchards will benefit the cone production (Gansel 1973; Werner 1975; Schmidtling 1983). Until more is known about the effect of site and cultural treatment on cone production of lodgepole pine, the current British Columbia strategy of concentrating seed orchards for the central Interior at Red Rock and for the southern Interior at Vernon appears to be appropriate biologically and economically. The results also suggest that the seed orchard for lodgepole pine from northern British Columbia and the Yukon probably should not be moved to south of latitude 56°.

Both seed- and pollen-cone production showed similar patterns of geographic variation, but the magnitude of differences among provenances was much larger for pollen than for seed cones as reflected in their ratio (table 3). Does this differentiation in sexual ratio among provenances represent the strategy of parental resource allocation, reflecting evolutionary fitness (Doust and Doust 1983)? Or is it environmentally induced due to geographic displacement (i.e., long day length conducive to pollen-cone production as a result of northern displacement) (Larson 1961; Giertych 1967)? Daylength is the prevailing factor affecting cone initiation following geographic transfer. In our case, the maximum northern transfer was about 3° of latitude, equivalent to the maximum increase of about 40 minutes in daylength occurring in June. It is unlikely that this relatively small change in daylength would have such a drastic effect on pollen-cone initiation (Mirov 1956).

The pollen-ovule ratio plays a central role in natural selection associated with sexual reproduction. It is well established that the pollen-ovule ratio increases with the increasing rate of outcrossing (Willson 1979; Doust and Doust 1983); with wind-pollination species, a large quantity of pollen production is probably the most effective way to ensure outcrossing (Willson 1979). That the differential pollen-seed-cone ratio among lodgepole provenances is related to their outcrossing rate appears to be in line with the results of Yeh and Layton (1979). They found the geographic trend of decreasing genetic variability among lodgepole pine populations extending from the southern Interior of British Columbia toward the Yukon Territory. However, it is still not clear why natural selection should favor high outcrossing rates in the southern Interior populations.

Differential seed- and pollen-cone production capacity among clones and geographic sources is of practical significance. First, a few prolific producers (particularly pollen cones) can affect the genetic composition of the seeds from seed orchards (O'Reilly and others 1982). Second, large clonal variation in cone production makes it difficult to achieve the goal of maximizing genetic gain while maintaining the cone production capacity at the time of seed orchard roguing. Third, the risk of pollen contamination increases if seed orchards for different geographic regions are proximally located. In the latter case, pollen contamination could consequently weaken the genetic adaptive capability of seed produced. For example, excessive contamination of the seed orchard for the northern and central Interior of British Columbia by the southern Interior sources can severely impair winter hardiness of progeny seed.

Information reported here is useful in guiding the selection of seed orchard location, projecting seed yield, and alleviating potential problems in lodgepole pine seed orchard management related to pollen contamination and clonal disparity in cone production. However, since the clonal banks and the w.p. progeny plantation are not planted at the same site and not specifically designed to address seed orchard management, questions such as the effect of site and cultural treatments on cone production and seed yield of lodgepole pine grafts and seedlings remain inadequately answered. A study designed to answer the above questions is now in progress. Information generated from this study will further our understanding about the flowering response of lodgepole pine grafts and seedlings under different environments.

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Section 4. Effects of Biological Factors On Seed Production

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INFLUENCE OF VERTEBRATES ON CONIFER SEED PRODUCTION

Curtis H. Halvorson

ABSTRACT: Many birds and mammals utilize conifer tree seed but few have feeding strategies or physical capabilities that allow for cone predation prior to seed dispersal.

The American red squirrel is the primary and most effective vertebrate cone predator, although chipmunks also forage in trees for food. Grizzly and black bears use conifer cones in limited fashion. Clark's nutcrackers can have a major impact on cone crops of large-seeded conifers. Jays, crossbills, siskins, and finches are other common bird predators but for most birds our knowledge of their impact is more anecdotal than measured. Low densities and erratic movements suggest most birds can only exert sporadic local pressure on cone crops but could be damaging to high-value seed orchards and production areas.

Red squirrel feeding on ponderosa pine and Douglas-fir cones begins in June and continues through summer, but clipping for storage is timed to seed maturation and starts in early August. Squirrel feeding removed 17 to 100 percent of the annual crop on an island, but a consistent correlation between crop removal and crop production was not found. Seedfall after squirrels' harvest ranged from 15,000 to 172,000 sound seed per acre in good years. Cone clipping by squirrels is often accompanied by loss of branch and terminal buds and first-year conelets. Vegetative parts of conifers may be used when crops fail.

Two highly adapted seed predators, the Clark's nutcracker and the pinyon jay, return some value by being effective seed predators. The cone caches of the most effective predator, the red squirrel, serve as a source of high quality seed for nurseries. The impact of most birds cannot be fully determined from the present, mostly descriptive, literature. And the red squirrel's inconsistent harvest of cone crops appears to be more influenced by weather, seed quality, and the availability of other food rather than simply by cone abundance or squirrel population density.

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INTRODUCTION

Many vertebrates are specialized predators on conifer seeds. Some are more dependent than others. Red squirrels (Tamiasciurus hudsonicus) cache cones in fall, prior to seed dispersal, so that they are assured of a dependable food supply through long boreal winters. The Clark's nutcracker (Nucifraga columbiana) gathers limber pine (Pinus flexilis), whitebark pine (P. albicaulis, and pinyon (P. edulis) seeds into throat pouches during the fall harvest and transports these as far as 14 mi (22 km) (Tomback 1977; Vander Wall and Balda 1977; Lanner and Vander Wall 1980) to ground caches. These become the winter and spring food supply for adult and juvenile nutcrackers. Vertebrate interest in conifers thus produces seed loss if the animal's role is primarily that of a predator, or seed distribution and tree regeneration if the role is primarily that of a disperser. These roles have been studied and will be included in my discussion of the influence of vertebrates on seed production.

Man's interest in seed includes an economic dependency that seeks to enhance seed production to produce wood commodities. We are interested in seed losses and have catalogued vertebrate influences and their control in the past. By 1915, according to Pank's (1974) bibliography on animals and tree regeneration, there were eight government and forestry publications discussing reforestation and vertebrate agent problems. Several hundred reports and numerous conferences have followed (Smith and Aldous 1947; Tevis 1953; Radwan 1963; Black 1969, 1974; Janzen 1971; Pank 1974). Most focus on post-dispersal seed loss and subsequent stand establishment, damage, and protection. The usual scenario is: cones open releasing seeds, which are gathered and consumed by rodents.

I will confine my review to those animals that reach the seed before it leaves the tree. This is predispersal impact and is far less quantified than that for shed seed. Those animals that have specialized adaptations for harvesting predispersed seed are primary influences. There are secondary influences on seed production--bears stripping cambium, porcupines (Erethizon dorsatum) girdling conifers--but I will confine descriptions to the primary agents. I will describe these adaptations and their effects and implications on seed reproduction. The birds and mammals discussed herein (table 1) are mostly residents

Table 1.--Vertebrates of the Inland Mountain West that use conifer seed prior to seed dispersal (Table modified from Smith and Balda 1979)

Taxonomic Group	Genera of trees	Method of using seed	References
BIRDS:			
Family:Picidae			
Hairy Woodpecker *Picoides villosus*	*Pinus*	Extracted seed from closed and open cones are eaten by adults and juveniles	Ligon 1973, Smith and Balda 1979; Stallcup 1968, 1969; Tomback 1977
White-headed woodpecker *Picoides albolarvatus*	*Pinus*	Extracted seed from closed and open cones are eaten by adults and juveniles	Curtis 1948; Ligon 1973; Smith and Balda 1979; Tevis 1953; Tomback 1977
Family:Corvidae			
Gray Jay (questionable) *Perisoreus canadensis*	*Abies*, *Picea*	"May extract seeds from open cones or retrieve from ground to eat and store as boli"	Smith and Balda 1979 list without evidence; see Dow 1965 for feeding test; Turcek and Kelso 1968 list European jay *P. infaustus*
Steller's Jay *Cyanocitta stelleri*	*Pinus*	Cache seed from open cones to feed adults	Benkman et al. 1984; Curtis 1948; Smith and Balda 1979; Tevis 1953
Pinyon Jay *Gymnorhinus cyanocephalus*	*Pinus*	Cache seed extracted from closed and open cones to feed adults and young	Ligon 1978; Smith and Balda 1979; Turcek and Kelso 1968
Clark's Nutcracker *Nucifraga columbiana*	*Pinus*, *Pseudotsuga*	Cache seed extracted from closed and open cones to feed adults and young	Benkman et al. 1984; Curtis 1948; Guintoli and Mewaldt 1978; Lanner and Vanderwall 1980; Smith and Balda 1979; Tomback 1977, 1980, 1981, 1982; Vanderwall et al. 1981
Black-billed Magpie *Pica pica*	*Pinus*	Cache seed from open cones and ground to feed adults	Smith and Balda 1979 (Vanderwall and Balda, unpublished)
Family:Paridae			
Black-capped Chickadee *Parus atricapillus*	*Abies*, *Picea*, *Pseudotsuga* *Pinus*	Cache seeds from open cones and ground to feed adults	Bent 1946; Curtis 1948
Mountain Chickadee *Parus gambeli*	*Abies*, *Picea*, *Pseudotsuga* *Pinus*	Cache seeds from open cones and ground to feed adults	Benkman et al. 1984; Haftorn 1974; Smith and Balda 1979; Stallcup 1968, 1969; Tevis 1953; Tomback 1977
Boreal Chickadee *Parus hudsonicus*	*Abies*, *Picea*, *Pseudotsuga*	Cache seeds from open cones and ground to feed adults	Haftorn 1974; Smith and Balda 1979
Family:Sittidae			
Red-breasted Nuthatch *Sitta canadensis*	*Abies*, *Picea*, *Pinus*, *Pseudotsuga*, *Tsuga*	Seeds from open cones cached and eaten by adults	Benkman et al. 1984; Curtis 1948; Smith and Balda 1979; Stallcup 1969; Tevis 1953
White-breasted Nuthatch *Sitta carolinensis*	*Pinus*	Uses and makes cache of seeds and finds seed on ground	Curtis 1948; Smith and Balda 1979; Stallcup 1969; Tevis 1953; Tomback 1977
Pygmy Nuthatch *Sitta pygmaea*	*Abies*, *Picea*, *Pseudotsuga*, *Pinus*	Seeds from open cones cached and eaten by adults	Ligon 1973; Smith and Balda 1979; Stallcup 1969
Family:Fringillidae			
House Finch *Carpodacus mexicanus*	*Pinus*	Feeding on opening cones and seed fallen on ground	Curtis 1948
Red Crossbill, White-winged Crossbill *Loxia curvirostra*, *L. leucoptera*	*Abies*, *Larix*, *Picea*, *Pinus* *Pseudotsuga*, *Tsuga*	Seeds from closed and open cones fed to adults and young	Bock and Lepthien 1976; Curtis 1948; Kemper 1959; Ligon 1973; Newton 1973; Smith and Balda 1979; Stallcup 1969; Stickney (1966 pers. comm.); Tomback 1977
Common Redpoll *Carduelis flammea*	*Pinus*	Feeding on opening cones	Bent 1968; Curtis 1948; Newton 1973
Pine Siskin *Carduelis spinus*	*Abies*, *Larix*, *Picea*, *Pinus* *Pseudotsuga*, *Tsuga*	Seeds from open cones and the ground fed to young adults	Benkman (pers. comm.); Bent 1968; Smith and Balda 1979
MAMMALS			
Order:Rodentia			
Red Squirrel *Tamiasciurus hudsonicus*	*Abies*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga*, *Tsuga*	Cache and feed from whole closed cones	Curtis 1948; Duncan 1954; Finley 1969; Gurnell 1984; Kemp and Keith 1970; Schmidt and Shearer 1971; Shaw 1936; Smith 1970; Smith and Balda 1979
Chipmunk *Eutamius*	*Abies*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga*, *Tsuga*	Cache and eat seeds from closed or open cones	Benkman et al. 1984; Broadbrooks 1958; Schmitz (1966 pers. comm.); Tomback 1977, 1981
Golden-mantled Ground Squirrel *Spermophilus lateralis*	*Pinus*	Forage for single seeds	Benkman et al. 1984; Smith and Balda 1979; Tomback 1977, 1981
Order:Carnivora			
Grizzly and Black Bear *Ursus arctos*; *U. americanus*	*Pinus albicaulis*	Major fall food from squirrel caches; some tree climbing by black bear	Kendall 1983; Mealey 1980; Murie 1981; Tisch 1961

of the geographic area prescribed for this symposium, the Inland Mountain West, lying between the east slopes of the Cascades and the western edge of the mixed-grass prairie in Alberta and Montana. Important knowledge of some bird species has come from adjacent areas; these and pertinent foreign literature are included where applicable.

Background References

Background information on animals and their use of tree mast has been reviewed by Janzen (1969, 1971-insects, birds, and mammals), Smith and Balda (1979-competition between animals for conifer seed), and Smith and Reichmann (1984-food caching behavior). Boreal forest birds, their Holarctic distribution and adaptations to coniferous forests, have been covered by Udvardy (1969), with emphasis on the Northern Rocky Mountains. The Corvidae (crows and jays), have special behavioral adaptations for food movement and storage, particularly conifer seeds, and these habits are reviewed by Turcek and Kelso (1968) for 22 European and North American species. Tree squirrels are the only mammals that relate importantly to tree mast. Gurnell (1983) has provided a major review of Palearctic and Nearctic tree squirrel behaviors and population responses to seed crops; Heaney (1984) included tree squirrels in summarizing climatic and latitudinal relationships to life histories of the Sciuridae. The nature of red squirrel cone caching, energy supplies, and some forest regeneration implications are described by Finley (1969). The evolutionary history of squirrels is thoroughly discussed by Black (1972), Emry and Thorington (1984), and Hafner (1984); Brodkorb (1971) describes the fossil record on birds. These reviews are useful references for readers seeking perspective on vertebrates and predispersed seed crops.

Some History

Modern conifers were geologically well-established in the Cenozoic Era about 70 million years ago (Egler (1977). Ancestors of our present birds and squirrels appeared much later, in the mid-Miocene, about 18 million years before present (ybp; Brodkorb 1971, Black 1972, Hafner 1984); by the Pleistocene, modern forms used conifer seeds much as we see them now. The adaptations between vertebrates and conifer seeds in the Inland Mountain West were already well established genetically when the late Pleistocene glacial ice sheets excluded most forests from the Northern Rocky Mountains, beginning 42000 ybp, and were maintained after re-establishment of forests as recently as 12000 or fewer years ago in some areas (Heusser 1969).

The adaptive behaviors of animals of the montane West stem from the seasonality of the taiga--the extremes in seasonal temperatures and moisture. Most birds migrate altitudinally at least, or latitudinally at most, in response to annual food shortages. Invertebrates disappear, most seeds and berries fall, plants dry and go dormant. A few, chiefly the corvids (crows, jays, nutcrackers), store food over winter whereas nuthatches (*Sitta* spp.) and chickadees (*Parus* spp.) do so only for days or weeks (Udvardy 1969). Red squirrels cache and defend their winter supply of cones (Smith 1968; Gurnell 1983) but chipmunks (*Eutamias* spp.) take their seed hoards to bed, packing several thousand at a time under and around their underground nests (Broadbrooks 1958). Bears (*Ursus arctos*, *U. americanus*) also take their food supplies into hibernation but as energy already assimilated as fat tissue. Man's economic concerns about vertebrate use of seed seldom reflect on the fact that animal use of seed is an evolutionary phenomenon enabling species to occur in certain geographic areas. It is difficult for us to comprehend the pace of adjustments that occurred during the coevolution of birds, mammals, and trees. Animals must adapt to external conditions of food abundance and scarcity or die, while man can create and, to large extent control, his own food supply and living environment.

Interactions: Mutualism and Defense

In recent years there has been renewed interest in vertebrate-seed relationships that goes beyond the economic aspects of seed-eating related to losses in tree regeneration. This interest has looked at seeds and their vertebrate predators as biological interactions between two organisms--the plant seeking effective mechanisms for reproducing and the vertebrate using the plant for survival. Negative interactions as coevolved defensive mechanisms were initially emphasized in this "new look" (Smith 1968, 1981; Janzen 1969, 1971; Elliot 1974). Janzen (1971) considered that trees are not entirely helpless and over time have envolved mechanisms to defend themselves. These mechanisms include satiating the predators and minimizing the feeding intensity (Janzen 1971). The entire seed crop could ripen synchronously and overwhelm the harvesting ability of predators, as Benkman and others (1984) concluded for southwestern white pine (*Pinus strobiformis*) and the red squirrels. If seed crop abundance occurs only at long intervals, and predator peaks lag the seed crop peaks, then predators whose population build-ups are related to seed crop abundance have reduced populations and less predation capability.

Another defense mechanism may be present in lodgepole pine (*Pinus contorta*). Cone serotiny and smaller, fewer seeds in the harder serotinous cones have been theorized as tree defenses against red squirrels (Elliott 1974; Smith and Balda 1979). The squirrels, in turn, develop heavier jaw musculature, according to Smith (1970, 1981). But if hard nuts and cones predate the origin of squirrels, a suggestion by Emry and Thorington (1984), then plants might first have developed some of their

defenses against geologically older factors such as insects or fire.

Odum recently (1985) advised against population ecology focusing on the negative interactions--competition and predation--and predicted more study of positiveness--cooperation and mutualism. Mutualism requires that the association between different organisms increase the fitness of both, not just one. The seed dispersal activities of fruit-eating birds and mammals examined by Krefting and Roe (1949) have been recognized as mutualism, as have pollinating insect interactions reviewed by Owen (1980). An argument has been made by Owen and Wiegert (1981) for the stimulating effects of grazer saliva and feeding on grasses. Owen (1980) further theorizes that removal of plant growing points, apical shoots and buds, is favorable to the plant because it induces branching, to the extent that a plant is better supported, photosynthetic parts are more favorably exposed, and seed production is increased by profuse branching. Although he does not mention squirrel clipping of terminal buds, it is an activity I have observed and will allude to later, as a factor in ponderosa pine (Pinus ponderosa) branch morphology. A recent paper by Tomback (1982) portrays this increasing interest in mutually beneficial coevolved relationships and provides substantial evidence that the seed dispersal activities of the Clark's nutcracker are more effective than that of rodents and other animal agents (see also Hutchins and Lanner 1982). The nutcracker caches whitebark pine seed in conditions particularly suited for germination and seedling survival and most likely to provide the best recruitment to the pine population. Favorable aspects of nutcracker caching include moving this heavy wingless seed away from under the immediate tree canopy, often into pioneering habitats such as burns, thereby reducing concentrations for rodent predators. In Utah a high elevation burn is being restocked with limber pine by the seed caching activity of Clark's nutcracker (Lanner and Vander Wall 1980). Similar beneficial relationships have been suggested between the wingless pinyon pine (Pinus edulis) seed and the pinyon jay (Gymnorhinus cyanocephalus) (Ligon 1978) but hard evidence to date shows the benefit only to the bird.

SEED AS FOOD

Seeds are a particularly efficient food resource for animals. They are a sessile prey that periodically occurs in large abundance, are durable to store, and have a dormancy that improves storage survival, particularly in the cooler temperate zones where caching behavior among birds and mammals seems more common (Smith and Reichman 1984). Viable conifer seeds, the condition animals normally select for, are uniform in size and have a clumped distribution when in the cone, making them highly visible and accessible to those animals having the physical abilities and feeding strategies adapted to using this resource in the tree. Conifer seeds have higher energy values when compared to seeds of most angiosperms; deciduous tree exceptions being shagbark hickory nuts (Carya ovata) and black walnut (Juglans nigra) whose 6302 and 7221 cal/g dry weight (dw) of endosperm and embryo (Smith 1970) is in the mean range (6781 ± 760 cal/gm dw) of 19 conifer species reviewed by Grodzinski and Sawicka-Kapusta (1970). Smith (1968) determined the average caloric value of eight conifer species to be about 7000 cal/g dw; ponderosa pine having the highest at 7558 (SD 132) cal/g dw and lodgepole pine the lowest at 6827 (SD 152) cal/g dw. The average value of 400 plant species seeds tested by Golley (1961) was 5065 (CV 219) g cal/g dw, although he included seed head and coat material. In conifer seeds the shell can constitute about 20 percent of a seed's caloric value (Smith 1970). The superior nutritive quality of conifer seeds comes from their high lipid content (Smith 1970) and lipids have the highest caloric content (about 9000 cal/g dw) of basic nutrition elements. Proteins average about 5000 and carbohydrates about 4000 cal/g dw (Smith and Follmer 1972). Smith (1970) recorded the digestive efficiency of two red squirrels at 90 percent on nut kernels and reported the digestive ability was about in proportion to the caloric value or lipid content. Fat is the principal food storage form in conifer seed (Rediske 1961) and a most durable form in cool storage such as a squirrel midden.

The importance of conifer seeds in the diets of their animal users is incompletely known. It has been explored for the red squirrel by Smith (1968) and Finley (1969) in speculative discourse, and for the Clark's nutcracker by Tomback (1982) more precisely. It is difficult to measure the total energy needs, use, and contribution of conifer seeds to free-living birds or squirrels and at present the relationships can only be crudely estimated. Anyone who has watched a red squirrel in daily activities can see they are extremely energetic creatures. Their basal metabolic rate is 1.76 times that expected for an animal its size (Irving and others 1955). The daily energy consumption for an adult male red squirrel in summer averaged 117 kg cal and for a lactating female 322 kg cal (Smith 1968). Five half-grown juveniles consumed about 25 percent (80.5 kg cal) of their mother's daily requirement during nesting. Smith calculated that a squirrel's territory contained nearly the average total estimated food energy required (42,700 kg cal-Finley 1969) by a squirrel. These figures are to be accepted with fair caution, as mentioned earlier. On the basis of a squirrel perhaps getting half its subsistence from other foods such as fungi, fruit, and flower heads, Finley (1969) provides estimates of the amount of seed needed from five conifer species for the other half of a squirrel's energy needs (table 2).

Table 2.--Estimated amounts[1] of seed needed to provide 21,350 kg cal, half of the annual energy requirement of an adult _Tamiasciurus_

	Douglas-fir	Engelmann spruce	Blue spruce	Ponderosa pine	Lodgepole pine
Thousand fresh whole seeds	400	1200	910	170	1300
Kg of fresh whole seeds	4.4	3.9	3.9	5.2	5.8
Kg of dry seed kernels	3.0	3.0	3.0	2.8	3.1
Number of cones	9200	--	--	2400	62,000
Bushels of cones	13	17	8.6	8.7	24
Number of good seed trees	8.5	14	17	6	47
Acres of forest	3.2	2.0	1.7	0.8	4.1

[1]The values in this table are internally inconsistent because they are derived from several independent sources. (From Finley 1969). Figures represent a broad linking of averages and areas to derive relations between quantities of seed, cones, trees, and area. Figures could be refined considerably through further study.

The Clark's nutcrackers studied by Tomback (1982) in the eastern Sierra Nevada recovered stored whitebark pine seed from about April to July and the total energy requirements were estimated at 16000-25500 kJ (min-max) or 133 to 213 kJ per day. These caloric requirements convert to 50 to 84 seeds per day, amounts a nutcracker can readily carry in its throat pouch. The red squirrel and Clark's nutcracker energy requirements have been more intensively evaluated than any other species I will discuss. Because conifer cone crops fluctuate considerably, the effects of the varying, highly nutritious food supply will be discussed later.

PREDATOR OR SEED DISPERSAL AGENT

Predispersal seed removal by vertebrates represents an interception in the normal cycle of a tree. A superficial judgment would class the act as predation and the agent as a predator. A distinction exists between seed predators and seed dispersers (Smith and Aldous 1947; Turcek and Kelso 1968); predators being those whose seed use results in seed destruction, as opposed to the seed dissemination effect of dispersers. Janzen (1971) judges the two roles according to the precision with which seed processing (i.e., completeness of assimilation) occurs, and whether the agent seeks the fruit or the seed. After passage through the gut of six bird and four mammal species, the fruit of 25 different woody plant species mostly showed either no viability loss or improved germination (Krefting and Roe 1949). Such processing inefficiency would class the vertebrate consumers as dispersal agents. Krefting and Roe (1949) also found that the dispersal role of many animals was enhanced because passage through the gut helped overcome seed-coat dormancy. In most cases the desired food item was fleshy fruit material rather than seed. With conifer cones, the seed is the sought-after food material and most vertebrate agents that gather conifer seed act primarily as predators.

Of the 44 mammals and 37 bird species listed by Smith and Aldous (1947) as North American conifer seed eaters, the red squirrel can be considered the primary predator because of its efficiency in cutting cones from trees (Tevis (1953; Smith 1970; Shearer and Schmidt 1970; Schmidt and Shearer 1971; Harvey and others 1980; Gurnell 1983; C. H. Halvorson unpublished), and deeply burying these under damp conditions that preclude seed release (Shaw 1936; Finley 1969). Other mammalian gatherers and eaters of predispersed seed are given lesser attention because either they do not forage on commercially important conifers, or they eat seed but also cache it in clusters that often are not recovered, and later germinate. Grizzly and black bears are in the first category because the large seeds of the non-commercial whitebark pine are eagerly sought (Tisch 1961; Mealey 1980; Kendall 1983). Chipmunks and golden-mantled ground squirrels (_Spermophilus lateralis_) eat but also pouch seeds and cache them in shallow pits, failing to recover some portions of those (Tevis 1952, 1953; Broadbrooks 1958; West 1968). Red squirrels do not have cheek pouches, and thus store whole cones that do not germinate, therefore their storage act is not that of dispersal.

Most notable in the role of a dispersing agent are some members of the crow family (Corvidae), chiefly the pinyon jay and the Clark's nutcracker (table 1), who distribute seeds away from the trees and cache more than they recover. Of course they also consume seed but when the gathering is done in years of seed abundance the birds bury more seed than they consume (Tomback 1982). The other bird families (table 1) recognized as conifer seed gathers and feeders from cones are finch-types (Fringillidae), nuthatches (Sittidae), chickadees (Paridae), and a few woodpeckers (Picidae). Some of these groups may cache seeds for short periods of days or weeks, as with chickadees and nuthatches (Kilham 1974; Sherry 1984), but for the most part the families other than corvids can be considered predators on predispersed seed.

SPECIES THAT FORAGE ON PREDISPERSED SEED

The manner in which vertebrates forage on predispersed seed has been described by Smith and Balda (1979) as: removing the entire cones and caching (squirrels); extracting seed from green or ripe closed cones, with some birds performing storage (woodpeckers, crossbills, jays); searching and extracting seed from opening or opened cones (chickadees, nuthatches, small finches).

The physical and behavioral adaptations to these foraging methods are the subjects of this section. None of the species discussed (table 1) are such extreme specialists that they subsists only on conifer seeds. The sporadic nature of seed crops would not have allowed survival. The crossbills (Loxia spp.) are most closely linked to conifer seeds, in feeding, reproduction and movement, but in common with the other birds listed, they also utilize buds and insects. Fungi are important to rodents (McKeever 1964; Smith 1968; Sanders 1983; personal observation) and bears eat carrion and forage on herbaceous vegetation, roots and berries (Tisch 1961; Mealey 1980; Murie 1981). Despite certain foods being especially sought, usually large-seeded pines, none of the birds or mammals have distributions confined to the range of any one tree species.

I have tried to limit the vertebrate list (table 1) to those whose primary feeding behavior is that of taking cones or seed from the tree. That does not preclude their also foraging on shed seed or clipped cones as secondary efforts. The five bird and two mammal families that forage on predispersed seed include at least 22 species of vertebrates (table 1). All those shown occur across the northern Rocky Mountains. The listing is based on Smith and Balda (1979) but omits species out of the range in question, such as the scrub and gray-breasted jays (Aphelocoma coerulescens, A. ultramarina), plain titmouse (Parus inornatus), and shrews (Soricidae) and mice (Cricetidae) that only use dispersed seed. Added are two bears--the grizzly and black; and three birds--the black-capped chickadee (Parus atricapillus), house finch (Carpodacus mexicanus), and common redpoll (Carduelis flammea). The additions are based on references not available or not included by Smith and Balda (1979). To the bird listings could be added Williamson's sapsucker (Sphyrapicus thyroideus), reported by Tomback (1977) to occasionally take whitebark and Jeffrey pine seed (Pinus jeffreyi) from cones, or forage on Arizona limber and southwestern white pine cones during opening (Benkman and others 1984). The pine grosbeak (Pinicola enucleator) was observed by Tomback (1977) as a subalpine transient in the Sierra Nevada, taking whitebark and Jeffrey pine seed from cones. This grosbeak has been recorded primarily as a bud, fruit, and catkin feeder (Bent 1968; Newton 1973). My inclusion of the gray jay (Perisoreus canadensis) and black-billed magpie (Pica pica) is based on Smith and Balda (1979) although the former species remains undocumented as a conifer seed feeder. The authors cite unpublished data that the magpie harvests pinyon pine in Utah where the Steller's jay (Cyanocitta stelleri) is absent. In feeding tests (Dow 1965) that deliberately exposed gray jays to conifer cones (Abies lasiocarpa, Psuedotsuga menziesii) the birds showed a weak but negative interest in cones compared to strong search effort on bark and rotted logs. The test timing (March and April) would have been at the extreme end of seed dispersal time (Schopmeyer 1974) for these conifers in the western ends of their range (British Columbia Cascades, Vancouver) and might have contained unsound seed, normally the last to shed. When later tested with lodgepole pine that had seeds visible in partly opened cones the birds pecked but did not attempt to extract them, despite the birds being without food several hours prior (Dow 1965). The European jay (Perisoreus infaustus) is cited in many accounts listed in Turcek and Kelso (1968:282) as taking and caching Siberian stone pine (Pinus siberica), Norway spruce (Picea abies) and other conifer seeds. Further study of the gray jay relationship with conifer seeds is desirable because it is a Nearctic winter resident throughout its range in the boreal forest (Udvardy 1969; Welty 1975).

In the inland West all species in table 1 are year-long residents in a portion of those states bordering Canada and southward. It is characteristic of resident species of the taiga or northern coniferous forest that they are mostly seed-and nut-eaters and insect feeders (Welty 1975). In Montana only the white-headed woodpecker (Picoides albolarvatus) is not a resident. However, many of the birds show altitudinal migratory behavior after breeding, moving between forest communities with the onset of harsh weather, or latitudinally from one region to another, sometimes showing irruptive behavior in response to food scarcity. True migratory birds of our northern coniferous forests outnumber the residents. Udvardy (1969) attributes this paucity of complete adaptation to the sharp seasonal changes and relatively recent and interrupted expansion of boreal forests during interglacial periods. The adaptations birds especially have made is to migrate, to shift their food habits between summer and winter, and to prolong food availability by storing it. Mammals also show these adaptations, but rather than migrate some are dormant during winter.

The species descriptions that follow are patterned after Smith and Balda's (1979) succinct presentation, which should be read for additional insight on competition between seed eaters.

Birds

Woodpeckers.--Only recently was the hairy woodpecker (Picoides villosus) described feeding on intact conifer cones in the tree. However, an early record from 1928 is cited by Bent (1939) that seed, mostly conifer, averaged 12 percent in the diet (not identified as being volume or occurrence) of a humid-forest west coast subspecies of the hairy woodpecker (P.v. harrisi). The origin of the seed was not disclosed and could have been from ground foraging which is out-of-character for this bird. Stallcup (1968, 1969) provided the first accounts after observing hairy woodpeckers perched and feeding on pine cone clusters.

Attacking only the upper surface of ponderosa pine cones with their bill, they hammered and pecked, sometimes twisting bracts loose from the seeds which were also pecked open instead of cracked as finches do. The feeding occupied about 65 percent of their foraging time from mid-October through February in this Colorado study. Early spring foraging on ponderosa pine was also observed by Ligon (1973), and occasional feeding on whitebark and Jeffrey pine occurs in the Sierra Nevada (Tomback 1977).

The white-headed woodpecker was recognized as a pine seed feeder in 1911 (Bent 1939). All reports (Curtis 1948; Tevis 1953; Ligon 1973; Tomback 1977) refer to feeding on the large seeded species: ponderosa pine, Jeffrey pine, sugar pine (P. lambertiana), and whitebark pine. Spring (April) foraging on ponderosa pine cones in Idaho consisted of a few birds foraging steadily through open second-growth pine, chipping cones open for seed while clinging to them. In early August the birds attacked the hard green cones and extracted unripe seed (Ligon 1973). Three females that Ligon collected in October had their stomachs 60-70 percent filled with pine seeds. Tevis (1953) describes late-August feeding on California sugar pine cones two weeks prior to ripening. Groups of four to six birds "slashed open every cone on which they alighted and ate the seeds, leaving deep vertical trenches....." He reported 34 percent (559) cones destroyed. They concentrated on certain trees, thus one pine lost 85 percent (252) of its cones. White-headed woodpeckers reach the northern and eastern limits of their range in Idaho (Burleigh 1972) and are not common in Washington, although they are residents there also (Jewett and others, 1953). The Williamson's sapsucker may be a conifer cone feeder (Tomback 1977; Benkman and others 1984), but this is not substantiated enough to assess the importance to regeneration. Of the woodpeckers listed, the white-headed presently appears to be the species most interested in cones and able to damage them in quantity.

Jays.--Despite not having real evidence that the gray jay is a conifer seed consumer, the "Whiskey Jack" is a ubiquitous and territorial inhabitant of northern coniferous forest. Yet their use of plant material as food is hardly known (Rutter 1969). They are well-known omnivores especially attracted to meat and camp scraps. Their particular attribute is the ability to store food amidst conifer needles and in and on tree trunks and branches (Dow 1965). This storage is achieved by orally manipulating food until it is completely coated with thick saliva to become a mucous pellet or bolus. The saliva allows adhesion to a substrate (Dow 1965) and would seem ideally suited for caching seed, but there are no records to that effect. Captive jays were unable to open sunflower seeds and gray jays seemed committed to a single bill-shoving motion when burying (in captivity only) or storing food. The hammering motion that is used by other seed feeding corvids to store or extract conifer seeds was never observed by Dow (1965). Smith and Balda's (1979) inclusion of the gray jay as a conifer seed eater seems unwarranted at present and I have included it only because of its congener, the European jay, a known seed user (Turcek and Kelso 1968).

Three other jays, Steller's, pinyon, and Clark's nutcracker, share typical jay characteristics of strong bills and feet, social system, and a food storage instinct. The Steller's jay remains the least studied of the three. Tevis (1953) described the Steller's foraging in sugar pine when cones opened, "launching" from a branch to strike a cone and dislodge seed which was seized in mid-air, carried to a limb, and the kernel pounded open. This jay travels in raucous groups, concentrating on trees with opening cones. Only Smith and Balda (1979) mention storage, and large flocking movements do not appear in the reviews previously cited. The Steller's jay seems to be an inconsequential seed predator from knowledge presently available.

Pinyon jays live and feed in close association with pinyon pine - juniper (Juniperus spp.) communities but also occur with ponderosa pine, a seed readily accepted in lieu of the infrequent pinyon seed crops (Bent 1946; Balda and others 1972; Ligon 1978; Schopmeyer 1974). They readily extract conifer seed (table 1) from green or opening cones by hammering in jay fashion; they bury seed clusters in pockets, and practice communal caching, usually on open, warm-aspect slopes. From 30-50 seeds at a time can be transported in a distensible esophagus. The food is used later in winter and as food for new hatchlings in early spring (Ligon 1978). These strong fliers search widely for food, up to 13 miles (21 km) daily (Balda and others 1972). These behavioral characteristics are quite similar to those in the Clark's nutcracker, but the pinyon jay shows a unique physiological adaptation to cone abundance that is shared with the red crossbill (Loxia curvirostra), a bird more distinctly associated with montane and boreal forest. Pinyon jays can be stimulated to breeding readiness and actual breeding by the presence of an abundant pine crop. Thus, Ligon (1978) found breeding readiness (gonadal development) in early December, February breeding after a large pinyon seed crop, and August breeding in the presence of a large maturing seed crop that was used to feed young. He reported this only for southwestern New Mexico and similar behavior in northern parts of the jay's range is unknown. Pinyon seed volume in stomachs reached 95 percent in December to 50 percent in May as birds continued to use caches, then tapered to 20 percent in summer until new seed became available.

The Clark's nutcracker is the most thoroughly studied of the predispersal seed-eating jays, partly because its eruptive migrations are

well-known (Davis and Williams 1964; Turcek and Kelso 1968; Bock and Lepthien 1976) and its seed storage behavior has been thoroughly documented, but only in the last 15 years (table 1). In contrast, its Palearctic counterpart, the Eurasian Nutcracker (Nucifraga caryocatactes), has a long record of observation on feeding behavior and population migration (Formosof 1933; Turcek and Kelso 1968) in conjunction with fluctuations in its primary food, the Siberian stone pine (P. cembra). The Clark's nutcracker is superbly adapted to feeding on conifer seeds year round and, like the Eurasian nutcracker, possesses a sublingual throat pouch (Bock and others 1973) to store and transport food. This is more highly specialized than the pinyon jay's expandable esophagus and holds about 20 ml (125 limber pine) of seed (Lanner and Vander Wall 1980). The nutcracker depends heavily on whitebark, limber, and ponderosa pine (and related Jeffrey) pine extensively (Curtis 1948; Tomback 1977, 1981; Lanner and Vander Wall 1980) but readily takes Douglas-fir (Pseudotsuga menziesii) in the absence of the larger-seeded species (Giuntoli and Mewaldt 1978; Fisher and Myres 1980; Vander Wall and others 1981). The typical foraging pattern was first delineated by Tomback (1977) in the Sierra Nevada. The adult birds began harvest from unripe closed whitebark pine cones in mid-July. Seeds were exposed by forcefully repeated stabs to loosen and tear off scales. Soft seeds were removed piecemeal and eaten or moved into the sublingual pouch by a backward toss of the head. Hardened ripe seeds were extracted whole at a rate of about one per 7 sec. after scales were twisted and broken off. Seed soundness was detected by "bill-clicking" or rattling the seed within the mandibles; unsound seed being discarded. Pouch contents averaged 77 whitebark seeds. Storage occurred initially in late August in high elevation subalpine habitat but flights were also made at this time to lower elevations in the Jeffrey and ponderosa pine zones, to store whitebark seed for winter use, and also to "test" lower elevation seed. Harvest and storage of subalpine whitebark seed ended about mid-October but many birds had already moved to lower elevation wintering areas to harvest ponderosa or Jeffrey pine. Because whitebark pine cones are indehiscent, the birds continued to forage on any available in winter. The seed recovery period at lower elevations was from late December to late March with young being fed cached seed starting very early in spring. Upon returning to higher elevations in early summer the birds used subalpine caches. Tomback (1977) concluded that these altitudinal movement patterns were comparable to those reported from Montana (Giuntoli and Mewaldt 1978). The onset of harvest on limber pine in Utah was also similar (Lanner and Vander Wall 1980).

From a full pouch of whitebark pine seed a nutcracker will successively distribute 3.7 ± 2.9 seed per cache, burying them at a mean depth of 2.0 ± 0.8 cm (Tomback 1982); caches of limber pine were similar (4.2 ± 3.1 seeds per cache at 2-3 cm depth (Lanner and Vander Wall 1980). Seed cache recovery apparently relies heavily on memory, supplemented by visual cues (see Tomback 1980). Eurasian nutcrackers can find stored seed under snow less than 2 m deep (in Tomback 1980). Olfactory detection was recently tested in another corvid, the magpie, and reported to show at least close distance effectiveness (less than 1 m) on cod liver oil (Buitron and Nuechterlein 1985). Corvid olfactory bulbs are quite small compared to birds with known olfactory capabilities.

The seed use pattern of Clark's nutcracker (and pinyon jay) is to store seed when it is seasonally plentiful (fall), with subsequent recovery when it is scarce but needed by nestlings (winter-spring). Conifer seed was the most important year-long food in 426 nutcracker stomachs examined from Montana (Giuntoli and Mewaldt 1978). Average importance of weighted samples from four years showed conifer seeds constituted 83 percent of stomach volume balance but occurred 59 percent of the time, mostly in summer. Ponderosa seed volume and frequency (52 percent, 80 percent respectively) were greater than whitebark (19 percent, 42 percent respectively) in this Montana study. The collection elevations between 3280-8500 ft (1000-2500 m) spanned the distribution of the pines in western Montana. Seed consumption was strongly influenced by availability. A bumper Douglas-fir seed crop in 1946 provided most of the fall-to-spring diet in the presence of only a moderate ponderosa cone crop. In 1948, a very heavy ponderosa crop was reflected by only those seeds occurring in stomachs between September 1948 through last samples from May 1949; this occurring with "moderate crops" of whitebark and fir present.

The black-billed magpie (Pica pica) is not cited as a conifer seed eater except by Smith and Balda (1979) who refer to unpublished data from Utah (Vander Wall and Balda) that the magpies take pinyon pine seed in the absence of Steller's jays. The magpie in Europe stores angiosperm nuts as does the yellow-billed magpie (P. nuttali) in California (Turcek and Kelso 1968).

Chickadees.--Chickadees (Parus spp.) are small tame birds resident to the coniferous forest of Canada and the U.S. They forage industriously on tree trunks, branches, foliage, and the ground, using their short, strong acute bills to extract and store arthropods, spiders, insects, and seed in bark crevices (Haftorn 1974). In searching open conifer cones they typically cling to the underside or hang upside down, grasping seed wings and tugging the kernel from between the cones scales (Bent 1946). All conifer species are used, including the larger seeds like ponderosa, limber, whitebark, and Jeffrey pine (Curtis 1948; Tomback 1977; Benkman and others 1984). The

black-capped and the mountain (P. gambeli) chickadee occur with conifer distribution in the West Coast Corderilleran and Rocky Mountain Ranges. The boreal chickadee (P. hudsonicus) is most common in Canada and Alaska but dips down into Washington and Montana. At least short-term (24 hour) memory has been demonstrated for the black-capped chickadee in relocating stored seed (Sherry 1984) and food storage allows prolonged predation. Although no evaluation of impact occurs in the literature, the chickadee, like other small seed-foragers (nuthatches, small finches) cannot engage closed cones and must concentrate seed gathering for the brief period between cone opening and seed shedding. It therefore seems unlikely that chickadees have much impact on predispersed conifer seed.

Nuthatches.--The nuthatches (Sitta spp.) (table 1) are behaviorally related to chickadees in many seed foraging mannerisms. Although the nuthatches are particularly adept at working up and down vertical surfaces in their search for insects they also mount open cones from all angles to pull seed out, eating it or storing by poking or hammering them under bark or into crevices (Bent 1948; Ligon 1968; Kilham 1974; Smith and Balda 1979). Species of both families search assiduously among foliage and branches but nuthatches feed on the ground less than chickadees and only occasionally probe fallen cones (Stallcup 1968; Smith and Balda 1979). Nuthatches and chickadees are winter residents in western coniferous forest and often form loose flocks with other seed eaters during the fall cone-opening period and during winter (Stallcup 1968, 1969; Ligon 1973). Foraging has been reported on the squirrel-dropped cones of sugar pine (Tevis 1953), and in the tree on ponderosa pine (Curtis 1948; Stallcup 1968; Ligon 1973; Smith and Balda 1979).

A food habits study of three nuthatch species (table 1) in western Oregon showed the bulk of their diet from May 1969 through February 1970 to be insects (Anderson 1976). Birds were collected from Douglas-fir and ponderosa pine forests but conifer seeds were not listed in their diet, or cone crops mentioned. Because seed-eaters are opportunists adapted to irregular supplies of tree seed it may not be evident in their diet some years. However, the red-breasted nuthatch (Sitta canadensis) was reported taking ponderosa pine seed in Idaho (Curtis 1948), spruce (Picea spp.), fir (Abies spp.), and pine in Arizona (Smith and Balda 1979), limber pine and southwestern white pine in New Mexico (Benkman and others 1984), and is the only nuthatch observed to hammer open pinyon pine seeds with its bill (Smith and Balda 1979). It is also the only nuthatch that is in the group of nine North American boreal tree-seed eating birds showing eruptive migrations (Bock and Lepthien 1976). The white-breasted nuthatch (S. carolinensis), although presented by Smith and Balda (1979) as having the least specialized diet, appeared with the red-breasted taking ponderosa seeds (Curtis 1948) and foraging on whitebark and Jeffrey pine cones in California (Tomback 1977). They also feed from fallen cones of sugar pine (Tevis 1953) and ponderosa pine (Stallcup 1968; Smith and Balda 1979).

The smallest nuthatch, the pygmy (S. pygmaea), occurs west of the Continental Divide up into southern British Columbia. Like the others, it has been observed storing ponderosa pine seed taken from cones on the ground and from the tree in late fall and through winter (Stallcup 1968; Ligon 1973). Smith and Balda (1979) describe its feeding rate on a ponderosa pine cone as one seed extracted per second and the entire cone searched in under one minute.

Nuthatches exhibit intense foraging behavior, like all bark-searching birds who probe for insects, and their strong, narrow, relatively long bills are quite suited to probe the parted scales of conifer cones. But their feeding capability is limited to open cones in the period after squirrels, jays, and crossbills harvest, and in company with chickadees and finches. They also appear to store seeds for relatively short periods (days), cannot carry any quantity beyond one or two seeds, and have an evolutionary orientation for storing in rather limiting locations (bark or tree-trunk crevices) (Smith and Reichman 1984). These characteristics suggest far less predator efficiency than that associated with jays or squirrels. Without more thorough evaluation of seed predation nuthatches probably can't be rated a serious factor in seed loss. The red-breasted nuthatch appears to be more dependent on conifer seed then the pygmy or white-breasted nuthatch because it periodically moves great distances beyond its normal timber habitat, as in 1969-70, when Bock and Lepthien (1976) saw red-breasted nuthatches working on cemetery fenceposts in eastern Colorado prairie far from any tree.

Finches.--Finches (Fringillidae) are agile birds who coordinate their feet and bills, parrots-like, to clamber over conifer cones and search for seed. A finch characteristic is a specialized bill that is internally grooved along each side of the upper mandible. The sharp rim of the bottom jaw fits into this groove to hold and crack seed, a process in which the tongue manipulates and holds the seed in position. Bills vary in groove width, jaw strength, and external shape, thus limiting the size, hardness, and location of seed that can be used by a particular species. The pine siskin (Carduelis spinus) uses its long narrow bill as tweezers to insert between and even pry open cone scales to pull out seed, an adaptation allowing it to exploit many conifer species (table 1; Bent 1968; Newton 1973) but the stubby-billed common redpoll and house finch are probably not as adept or efficient at cone-feeding.

The hooked, crossed tips of crossbill (Loxia spp.) mandibles are uniquely formed to extract seed from hard, closed cones of most conifers, but the shape precludes ground foraging since the tips do not converge enough to grasp small seed. For closed cones the bill tip is inserted behind a scale and the lower mandible moved sideways by powerful muscles to separate the scales and release the seed. Then the specially adapted tongue (longer than other finches with an extra piece of cartilage on the end) scoops the seed out. Closed cones are usually wrenched off the branch and fed on while perched, using one foot as a clamp. According to Newton (1973) crossbills usually take only a few seeds from closed cones then drop the cones. These show frayed and split scales. At seed-dispersal time, crossbills feed while clinging to the cone, similar to other birds.

None of the finches store food, unlike all but the woodpeckers in table 1. This means they do not have a "banking" mechanism to prolong seed predation beyond the dispersal period. With few exceptions the Inland West conifers disperse most of their seed between late August and November. Trees that do extend seed dispersal into winter or longer, and can provide winter food, include western larch (Larix occidentalis), blue spruce (Picea pungens), west coast Douglas-fir (Pseudotsuga m. var. menziesii), western hemlock (Tsuga heterophylla), and the P. p. scopulorum variety of ponderosa pine in Colorado (Schopmeyer 1974). The indehiscent whitebark pine cones can retain seed for months if squirrel or jay predation is not complete. Serotinous lodgepole pine is seldom included as seed prey for birds because cones would either be impenetrable for most birds or an energy-inefficient food source. Lodgepole pine seeds were only 2 percent of the cone weights measured by Smith (1970), compared to 7.4 percent (Douglas-fir), 11.1 percent (ponderosa pine), 14.5 (Engelmann spruce), and 25.9 percent (subalpine fir--Abies lasiocarpa). Animals obviously benefit more by feeding efforts that secure large seed.

Red crossbills were observed near Missoula, Montana, fluttering around ponderosa pine cones and extracting seed from them on 9 May 1966. About the same period, farther west, chipmunks (Eutamias spp.) were seen up in ponderosa pine, clipping cones that retained seed from the 1965 crop (P. F. Stickney and R. F. Schmitz, pers. comm.). Ponderosa pine normally sheds 90-95 percent of its seed between September and the end of October in Idaho and western Montana (Fowells 1965; Shearer and Schmidt 1970). The year 1965 was particularly cold and wet from March through October, with the coldest September in 86 years. The remaining winter was one of the mildest on record. Dispersal of the 1965 seed crop apparently was unusually delayed by these climatic conditions, allowing extended foraging.

Seed can be exposed longer to predispersal predators when a wet fall inhibits cone opening. Normally, seed is released by a drying process where the scale fibrils shrink and contract, to draw the scales apart (Harlow and others 1964). Scale spreading takes place gradually over days and weeks and varies within and among individual trees. Cones also open and close, depending on humidity, causing discontinuous or delayed shedding beyond the normal dispersal period, at least for spruce, pine, and Douglas-fir (Shearer and Schmidt 1970; Allen and Owen 1972; Schopmeyer 1974; Hoff and Coffen 1982).

Irregular seed production and aberrant dispersal patterns are the norm however, and the foraging pattern for finches is most nearly a catch-as-catch-can matter. Such is reflected both in the intensity of seed-foraging and the restless movements of particularly the crossbills and pine siskin. Curtis (1948) singled red crossbills out as the most "voracious" feeders, present in the largest numbers, among nine bird species that descended on a medium-heavy ponderosa cone crop near Idaho City, Idaho, starting about 10 September 1947. Feeding birds persisted until early November in groups up to 40, although numbers peaked in mid-October. A rapid buildup of red crossbills also occurred at Yellow Bay Biological Station in western Montana between Aug. 1-15, 1954 (Kemper 1959). The population showed both physiological (gonadal) and morphological (brood patch, enlarged cloaca) breeding signs. These changes were attributed to excellent cone crops among Douglas-fir, grand fir, and Engelman spruce, and a moderate ponderosa pine crop.

Mammals

The Order Mammalia contributes relatively few vertebrates to the group who take seed in the tree, if compared to birds (table 1). The flying squirrel of the west (Glaucomys sabrinus) is endemic to coniferous forests but is omitted from my listing because I found no firm data that established its conifer seed eating activity, much less using cones still in the tree. Four flying squirrels nearly starved on an ad libitum diet of white spruce (P. glauca) seed, preferring laboratory chow and many other foods instead (Brink and Dean 1966). By contrast, red squirrels preferred spruce cones over the chow, taking 2-3 weeks to adapt to the processed food. Stomach contents of flying squirrels collected each month in California conifer stands showed year-long use of chiefly fungi and lichens but no seed, despite conifer seed being easily available in fall (McKeever 1960). Tests of flying squirrel food preference by Laurance and Reynolds (1984) did find they readily accepted pinyon nuts. Additional study is required because flying squirrels have been popularly accused of damaging conifers by clipping branches and terminals if not cones (Tom Lawrence, pers. comm.).

Red Squirrel.--As an acknowledged seed predator wherever it lives in North America (Murie 1927; Hatt 1929, 1943; Tevis 1953; McKeever 1964; Brink and Dean 1966; Smith 1970; Harvey and others 1980; Benkman and others 1984; Smith and Reichman 1984), the red or pine squirrel (table 1) cuts cones of all conifer species and stores them in winter larders or middens (Murie 1927; Finley 1969; Smith and Reichman 1984). These middens provide necessary energy for over-winter survival. They also supply sustenance needed during the later winter-early spring breeding period when other food is scarce. Each squirrel normally has at least one primary and several secondary middens (C. H. Halvorson, unpublished) which, in abundant crop years, are stocked with as many cones as can be secured prior to seed shedding.

In heavy seed years squirrel caches can supply food well into the second year beyond the crop harvest (C. H. Halvorson, unpublished), thus, the effect of a crop failure is not immediate. With such a food supply concentrated at great effort, it is understandable why squirrels call aggressively if intruders pass through the area of harvest. Red squirrel aggressiveness has long been considered territorial defense. Smith (1968), in southern British Columbia, has described territory size as varying inversely with food abundance but defended all year. Unchanging territorial boundaries were depicted by Rusch and Reeder (1978) in Alberta spruce and pine. Territoriality in a Colorado lodgepole pine forest was not dependent on large central stores because middens were highly variable in size and cone content (Gurnell 1984). Lodgepole pine stands differ from most conifer forests because a seed supply is always available in serotinous cones on trees, as well as in squirrel caches. My studies (C. H. Halvorson, unpublished) suggest that territorialism in the rigid sense of Smith (1968) may not be a constant nor perhaps appropriate concept to describe red squirrel behavior, although it certainly can be a perception. I have found food supplies to be defended and competition existing for areas in which middens were prominent features. However, the degree to which defense took place was more dependent on season, on population density, and on the year of the conifer seed supply than on a sustained and perpetual reactiveness. Their territorial calling (Smith 1978) is never a seasonal or yearly constant. However, red squirrels are solitary year-long, except for an apparent one-day mating period (Smith 1968). Therefore exclusiveness, how and whenever achieved, is distinctive to the species.

Red squirrel tree nests (less commonly underground) are globular and composed of grass, moss, needles, and twigs. The nest is usually one of several in the same or nearby tree. Nests and primary middens are always in proximity, usually 50 ft or less.

Published figures of red squirrel densities from across its geographic range are reviewed and tabulated in Rusch and Reeder (1978). Spring densities varied from about 1 acre (0.4 ha) per adult squirrel in spruce to 19.8 acres (8.1 ha) per squirrel in eastern hardwoods. In my 12-year study (unpublished data) minimum and maximum densities in Douglas-fir/ponderosa pine were 4.5 acres (1.8 ha) to 0.8 acres (0.3 ha) per adult in spring and slightly higher in fall, on the average. This variation illustrates the nature of squirrel populations--they can fluctuate greatly between years. This variation seems universal in tree squirrel populations (Gurnell 1983; Heaney 1984), and is often associated with tree seed abundance (e.g., Sciurus vulgaris in Finland - Rajala and Lampio 1963; T. hudsonicus in Alberta - Kemp and Keith 1970) in theory but not by proven hypotheses.

The red squirrel's characteristic cone clipping on ponderosa pine and Douglas-fir starts almost tentatively in late June and early July after seed fertilization. Douglas-fir and ponderosa pine cones are cut and peeled, usually in the tree or on a favorite feeding log or stump. The time at which red squirrel primary use of cones shifts from feeding to caching coincides with seed maturation, as it does with the Clark's nutcracker (C. H. Halvorson, unpublished; Tomback 1977). Seed maturation is marked by biochemical changes, the more important being a sugar content decrease and a fat increase in the endosperm (Rediske 1961). As mentioned earlier, fat resists spoilage, especially in the cool sites that squirrels select for middens (Shaw 1936; Hatt 1929; Finley 1969). Adult squirrels usually sever and drop individual cones from the branch, but ponderosa pine cones, being tightly appressed to each other and the shoot, are often dropped by cutting the branch just behind the cluster. This causes loss of cone primordia and any first year cones, and could remove three years of fruit growth. If the cluster happens to be on the terminal shoot, the trees's primary elongation point is also lost. Cone clipping rates can be rapid, almost frantic, and squirrels ignore their early morning and late afternoon bimodal daily activity pattern to work through the day. I have seen squirrels cutting Douglas-fir cones at rates of 4 to 8/min, and eating one cone each 3 minutes for 90 minutes. Giant sequoia cones were cut at rates from three/min to 538 in 30 minutes, or 18/min (Harvey and others 1980). Ponderosa pine cones are often cut and stored individually while fir usually are dropped, to be stored later. In one instance it took about 6.5 min per ponderosa pine cone from cutting to burying.

The quality of cones cached by squirrels is sometimes questioned. White spruce and Douglas-fir cones gathered from stores during the entire caching period were found to be ripe and have better viability than seed collected directly from trees in the same periods; there was no significant increase in viability with later dates of cutting, compared to collections

begun at the onset of major caching (Lavender and Engstrom 1956; Wagg 1964). Similar testing apparently has not been done for ponderosa pine or other conifers. Where cones ripen asynchronously between trees a question arises whether squirrels concentrate first on those trees whose mast ripens first. Olson and Silen (1975) found that coastal Douglas-fir seed showed steady weight increases and improved germination even during the final two weeks prior to seedfall.

Considerable data on cutting variability were gathered during a study of squirrels and cone crops on an island in Flathead Lake in western Montana (Halvorson and Engeman 1983). The years 1962 and 1965 had similarly dense fall squirrel populations, averaging >1/acre (>2.5/ha, fig. 1) between August and November. Roughly 65 percent of the cones counted on marked sample limbs were cut each year, although the number of cones on the limbs differed considerably (fig. 1). A heavy seed crop was produced in 1962, measuring about 11 lb/acre (12 kg/ha) of high quality (61 percent sound) seeds of Douglas-fir and ponderosa pine combined. 1965 had a very light crop (0.30 lb/acre, 0.34 kg/ha), consisting almost entirely of low quality (22 percent sound) ponderosa pine seed. In 1962, the Douglas-fir cutting rate was 8-10 days earlier than for pine, a typical pattern because ponderosa pine cones opened later than fir. By September 10, 1962, squirrels had gathered 179 pine and 636 fir samples cones, or over three-quarters of the sample ultimately removed that year. In contrast, in 1965, only 78 pine cones were cut by September 20 and only 90 total removed, at a desultory rate (fig. 1), by a larger population than present in 1962. Weather in 1962 was a "normal" warm but somewhat dry fall, and 1960 and 1961 had been poor crop years. 1965 had record September cold temperatures and a wetter than average entire year, causing seed to be held in cones (see earlier). In 1965, middens (caches) were still full from a 1964 seedfall of 28 lb/acre (31 kg/ha), the largest in 12

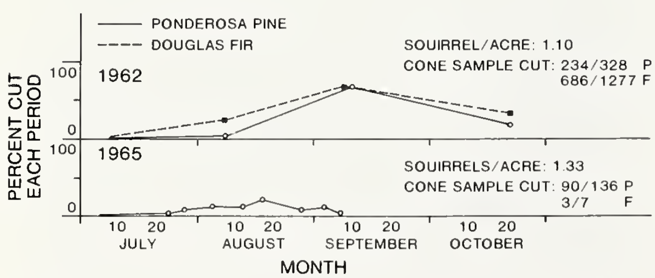

Figure 1.--Variability in cone-clipping rates on tagged-limb samples of ponderosa pine (P) and Douglas-fir (F) cones in a year of heavy (11 lb/acre; 12 kg/ha) cone crops and warm, dry, fall weather (1962), and poor (0.3 lb/acre; 0.34 kg/ha) cone crops and very wet, cool fall weather (1965). Similarly high squirrel densities occurred both years. Cedar Island, Montana (C. H. Halvorson, unpublished).

years. That seed was 60 to 70 percent sound. This example depicts the influence of weather, seed quality, and the availabilty and influence of previously stored food. To 1965 could be added the greatest abundance of fungi found on the island to that time--an effect from the "unusual" weather that year. Squirrels are known for their catholic food habits (Hatt 1929), especially utilizing the seasonal abundance of fungi and hanging it in trees to dry (Hatt 1929; McKeever 1964; Fogel and Trappe 1978).

Other Squirrels.--Chipmunks and golden-mantled ground squirrels are terrestrial rodents who forage extensively on the ground for seed, fungi, fruit, herbaceous material, and insects (Tevis 1952, 1953; Broadbrooks 1958). Both genera have internal cheek pouches that are effectively used to transport food. Over-wintering strategies differ in that the ground squirrel converts its fall feeding into fat layers metabolized during true hibernation. Chipmunks do not accumulate fat or gain weight before winter but go into torpor that may be interrupted by mild periods during winter. Their strategy of lining their underground nests with seeds allows them ready and safe access to nutritious food during winter awakenings. Broadbrooks (1958) described finding 1080 ponderosa pine seeds in one nest and 5360 Douglas-fir plus about 10,000 herbaceous seeds in another. One cache contained 170 g of seed, about 50 g being pine.

All studies of seed eating in these two genera have dealt with ground foraging for seed and those impacts on tree regeneration (Pank 1974). Seed predation in the tree canopy has been observational and anecdotal, thus we have no measure of its importance, and only sparse data that such foraging occurs. Spermophilus lateralis and Eutamius spp. have been seen foraging up in conifers. The chipmunks are more agile and seed constitutes a larger part of their diet than it does for the ground squirrel (Ingles 1965). E. amoenus has been seen feeding at heights to 100 ft (30 m) in ponderosa pine and Douglas-fir, pulling seed out as cones opened. Broadbrooks (1958) described two chipmunks feeding side by side from the same cone 50 ft (15 m) up in a tree. Whitebark and Jeffrey pine seed were gnawed from cones by golden-mantled ground squirrels and chipmunks in trees amidst seed-gathering by Clark's nutcrackers (Tomback 1977). Benkman and others (1984) in Arizona reported similarly for the two sciurids feeding on limber pine. These reports all describe fall feeding. Dick Schmitz's observation on ponderosa pine seed retained into at least early May and being used by chipmunks was mentioned earlier. None of the accounts I found mention any in-tree behavior other than pulling seeds from opening cones or gnawing cones. Some seed is probably pouched and carried to storage but cone-clipping and caching, a much more efficient form of foraging behavior (Janzen 1971; Smith and Balda 1979; Smith and Reichman

1984) is not discussed. The habit of seeking and pouching individual seed for storage is an evolved feeding characteristic, therefore the most efficient practice for terrestrial sciurids. Cone storing or clipping has not been the adaptive path taken by the chipmunk and ground squirrel, therefore is probably energy-inefficient for them and they would seem to impose minor impact on predispersed seed compared to arboreal squirrels.

Bears.--What is written on bear use of conifer seed in the Inland West comes mainly from Yellowstone National Park (Mealey 1980; Murie 1981; Hutchins and Lanner 1982; Kendall 1983) and northern Montana (Tisch 1961). Both the grizzly and black bear (table 1) eat whitebark pine seeds and berries as the main fall food, when available. Spring use of pine seeds is also a matter of availability if the previous fall had a heavy cone crop (Kendall 1983). Limber pine seeds are mentioned as grizzly food only by Craighead and Craighead (1972) and C. Jonkel (pers. comm.). The seeds are obtained by robbing red squirrel cone caches or rodent seed stores (Mealey 1980; Hutchins and Lanner 1982; Kendall 1983) but relatively little by climbing trees (black bear only--Tisch 1961). Therefore, bears would be secondary predators on cones and only on two noncommercial pines. Murie (1981) in Alaska suggested that spruce cones were not palatable, otherwise they would be expected to appear in grizzly droppings during heavy crop years when squirrels pile cones above and underground. Both bear species are able to extract seed without ingesting cones scales, therefore scales don't appear in scat. Bears feed by breaking cones up in their mouth or underfoot, then licking the seed up and expelling scales from sides of the mouth (Kendall (1983). In summary, bear feeding concentrates on noncommercial pines, depends mostly on squirrels storing cones, and is tied to periodicity of good cone crops. At least the two large-seeded pines are recognized as very important fall foods in the northern Rocky Mountains, and are sought after in spring prior to herbaceous vegetation growth (Kendall 1983).

VERTEBRATE IMPACT ON PREDISPERSED SEED

The known impact that vertebrates have on reducing potential seed crops depends on factors of economics, species characteristics that contribute to feeding efficiency, amount of study, and the response or dependencies of animals to crops. To portray relative importance, I have distilled from the foregoing accounts those qualifications that potentially affect or relate to species relative impact (table 3).

Judging Importance

The categories of table 3 list: 1) whether the species has been studied with the purpose and detail needed to quantify their effect on seedfall, has been only described, or has not been observed in measurable terms; 2) the economic status of food trees; 3) specialized and efficient feeding behaviors (beyond simply extracting seed from cones in trees or moving normal distances to exploit a food source, once located); 4) unique morphological adaptations that increase foraging effectiveness (beyond standard family attributes like gnawing incisors or grooved bills). The fifth category concerns responses to seed crops rather than impacts. It infers the importance of cones to animals by listing some responses that occur from cone scarcity or abundance, but also suggests the extent of evolutionary adaptiveness to cone crops. Winter residency is not shown in table 3, but would qualify a bird as a potentially more effective predator than transients. The white-headed woodpecker is the only bird listed whose eastern winter range stops at western Montana.

Species importance can be interpreted from table 3 by tabulating the number of categories having a positive (yes) statement and how many "Special" factors are assigned. Animals feeding on noncommercial whitebark, limber, or even the commercial seed of pinyon pine (Fowells 1965) would be of little concern to the timber industry regardless of how well studied the animals were. Thus, bear use of whitebark pine cones would be of major interest only to agencies managing these omnivores, especially since bears are secondary predators on cone crops. Siskins and redpolls would be of less relative importance even though they double their breeding period in response to unusually abundant spruce seed (Newton 1973), but they only feed exploitatively without caching when a crop appears. However, both species show irruptive migration and their impacts have not been measured. Benkman (pers. comm.) classed the pine siskin as a major but temporary predator on tamarack (Larix larcina), its competitor being the white-winged crossbill. Nuthatches and chickadees are birds that simply pull seed out and cache them individually in bark crevices, as they do other prey. The pygmy nuthatch is reported to extract one ponderosa pine seed/sec. and work one cone/minute (Smith and Balda 1979). Their impact is far less than the crossbills' who can attack closed cones effectively with their laterally abducting mandibles, irrupt, and breed as a result of stimulus effect from abundant cones (Kemper 1959; Newton 1973; Bock and Lepthien 1976). Although finches exploit but do not store food, the crossbills especially are extremely effective predators because they range widely in large flocks and can open cones. In high-value sites, such as seed orchards and nurseries, they have potential to consume large amounts of seed on a local basis (Curtis 1948). Their feeding potential is unmeasured.

The Important Vertebrates

Any bird or mammal that feeds on open and closed cones of commercial tree species, has

Table 3.--Status[1] and ordering of factors that relate predispersal seed users to conifer cone crops

Species	Impact & Feeding Quantified	Commercial conifers	Special feeding behaviors	Special morphology	Special Response to cone crops
Hairy Woodpecker	No	Yes	Closed and open cones	Strong bill, feet	Unknown
W.-headed Woodpecker	Yes-limited	Yes	Slash green cones	Strong bill, feet	Unknown
Gray Jay	No	Unverified	Not conifer seed	Salivary glands	[2]
Steller's Jay	No	Yes	No	No	Unknown
Pinon Jay	Yes	Yes-limited	Disperse caches	Esophagus expands	Breeding (SW only)[2]
Clark's Nutcracker	Yes	Yes	Disperse caches	Sublingual pouch	Breeding, weight[2]
Blk.-billed Magpie	No	Unverified	No	Buccal cavity	Unknown
Blk.-cap. Chickadee	No	Yes	Cache seed	No	Unknown
Mtn. Chickadee	Descriptive	Yes	Cache seed	No	Unknown
Boreal Chickadee	No	Yes	Cache seed	No	Unknown
Red-brst. Nuthatch	No	Yes	Cache seed	Strong feet, bill	[2]
W.-brst. Nuthatch	No	Yes	Cache seed	Strong feet, bill	Unknown
Pygmy Nuthatch	Descriptive	Yes	Cache seed	Strong feet, bill	Unknown
House Finch	No	Yes	No	No	
Red, W. Crossbills	Descriptive	Yes	Closed and open cones	Prying bill	Breeding[2]
Common Red Poll	No	Yes	No	No	Breeding[2]
Pine Siskin	Descriptive	Yes	No	No	Breeding[2]
Red Squirrel	Yes	Yes	Cache cones	Wrist joint	Breeding, longevity
Chipmunk	Descriptive	Yes	Cache seed	Cheek pouch	Unknown
G.M. Grd. Squirrel	No	Yes	No	Cheek pouch	Unknown
Grizzly & Black Bear	No	No	Rob squirrel caches	No	Concentrate feeding

[1] For European corvids (jays and crows) see Turcek and Kelso 1968.
[2] Periodic irruptive movement and (generally) southward invasions (Bock and Lepthien 1976).

particularly effective feeding behaviors and morphology, and shows a distinctive response that suggests strong dependency on cone crops would qualify as the potentially most effective predator on predispersed seed. These criteria quickly narrow the list to four vertebrates: the white-headed woodpecker, pinyon jay, Clark's nutcracker, and red squirrel (table 3). The white-headed woodpecker's propensity and efficiency in slashing open green cones (Tevis 1953) suggest they be especially identified in seed orchard management, the same as crossbills. White-headed woodpeckers have been studied little and their importance to cone crop impact is undetermined.

For the most part bird foraging on conifer cones is scattered and sporadic throughout forest stands during seed ripening, and is not conspicuous like that seen in cultivated crops (ducks and grain, blackbirds on rice and sunflower seeds) where loss is assessed in bushels or tons. Even concerted effort by researchers often achieves only approximations of agricultural seed loss (J. Besser, pers. comm.). However, some quantitative estimates of seed removal by Clark's nutcrackers and pinyon jays have been possible because the seed capacities of the nutcracker's sublingual pouch and the jay's distensible esophagus are known. Swallowing a seed completely or pouching it is distinguishable by the slight backward head toss which accompanies pouching (Tomback 1977). By counting the number of daily trips an individual nutcracker made with filled pouches, Tomback (1982) was able to estimate seed take. A single bird might store about 32,000 whitebark pine seeds in a good crop year, or 3-5 times its energy requirements, thus leaving seed for germination, rodent food, and other fates. Twenty-five birds foraging their average 4.5 hr/day for the approximate 42 day storage season were estimated as caching about 800,000 seeds (18,000 cones) in a 125 acre (50 ha) area. This was about 200,000 seed caches. From 75-100 percent of the whitebark pine cones were destroyed or partly eaten by nutcrackers and chipmunks in 1979 on Tomback's (1981) tree transects. Similar high losses of limber pine cones occurred in Utah where 90 percent (1322) were removed in 1979 and 70-90 percent even in the preceding bumper crop year (Lanner and Vander Wall 1980). The major result of unrecovered seed caches that germinate is the frequently seen multiple stemmed occurrence of whitebark pine. Tomback (1977) found 1 to 4 (mean 1.7 ± 1.0) seedlings per cluster in a Sierra Nevada burn where nutcrackers were storing seed. This corresponded to the average of 3.2 ± 2.9 (minimum 1 to maximum 15) seeds per cache recorded. Multiple-stems are also frequent on a Utah burn where nutcrackers are similarly reestablishing limber pine (Lanner and Vander Wall 1980).

Ligon (1978) observed flocks of 200 to 300 pinyon jays and calculated conservatively that they stored 30,000 seeds/day and perhaps 4.5

million seeds in the September-January storage period. He noted they frequently select very open areas (e.g., areas cleared of pinyon-juniper) to store seed next to shaded, moisture-favorable sites such as bushes or downed trees and away from competition with the parent tree.

Cone ripening phenology is a factor in seed loss --the "satiation" principle mentioned earlier. Benkman and others (1984) speculated that nutcrackers could take 6.6 percent of a limber pine seed crop because the cones appeared to ripen simultaneously on individual trees but asynchronously among trees. But if cones on all trees ripened together, which they interpreted for southwestern white pine, foraging would not encompass the entire crop before seed shed and only 3.7 percent would be harvested. Because seed-eating birds tend to concentrate their harvesting in flocks, seed loss would depend on seed-ripening patterns of conifers. Total loss contribution from birds is also related to the presence or absence of tree squirrels. Red squirrels took about 80 percent of an Arizona limber pine crop and nutcrackers harvested about 1.6 percent, whereas the birds gathered 12-22 percent when squirrels were absent (Benkman and others 1984). In assessing the impact of vertebrates on predispersed seed, the cone ripening pattern of conifer species should be identified and the contribution of seed-cache germination to re-establishing tree stands should be considered.

The Red Squirrel As A Cone Predator

The red squirrel's superior efficiency as a predator stems from its ability to rapidly collect large quantities of seed by cutting cones. The Clark's nutcracker and pinyon jay also gather seed in groups but their seed extraction and storage does not appear as efficient. I timed a red squirrel cutting ponderosa pine cones and carrying them from the tree to a cache and back at 6.5 min/ cone (6 cones). This equaled one seed stored each 6.5 sec, using a figure of 60 sound seed/ cone (Schmidt and Shearer 1971). It took nutcrackers an average of 24 (11-66) min to harvest one pouch load (77 seeds) of whitebark pine and return from caching them; an average of 19 sec/seed (Tomback 1982). However, whitebark pine seed is 4.6 times heavier than ponderosa seed (Schopmeyer 1974), reducing the weight equivalent carried to about 4 sec. But nutcrackers took 31 sec to extract seed from closed cones (7 sec for open ones) where the cutting rate for squirrels is unaffected by cone stage and squirrels harvest continually through the day in the presence of cone abundance. Nutcracker harvesting conservatively takes 4.5 hr/day (Tomback 1982). Guintoli and Mewaldt (1978) only recorded 25 ponderosa seeds per pouch (n=20) in Montana, suggesting far less efficiency than Tomback measured. A radio-collared squirrel (C. H. Halvorson, unpublished) was tracked for 90 minutes during which time it cut, peeled, and consumed the seed of 30 mature but closed Douglas-fir cones, i.e. 1 seed/4 sec or 3 min/cone, including some movement to reach cones in the trees. In other observations squirrels cutting an average of 6 (4-8) fir cones/min were removing 270 seed/min or 1 seed/1.3 sec. (about 45 seeds/cone using Finley 1969). The fact that squirrels guard their caches and caches are available only to bears increases greatly the squirrel efficiency.

The proportion of a cone crop harvested by red squirrels varies considerably and the effect on seedfall is not stated simply. Many harvest figures can be quoted: sugar pine 54 percent (Tevis 1953); limber and southwestern white pine 75-83 percent (Benkman and others 1984); ponderosa pine 19-82 percent (Schmidt and Shearer 1971); Douglas-fir 17-100 percent (C. H. Halvorson unpublished). Tevis (1953) noted that the harvest on individual trees also varied from 11-100 percent. In a study of ponderosa pine cone loss factors in Montana (Schmidt and Shearer 1971), the amount of cutting by squirrels could not be related directly to crop size but may have been affected by both the abundance of the companion conifer, Douglas-fir, and the weather. The pine cone harvest was inverse to the size of the fir crop. With a 1954 heavy fir crop (229,000 sound seeds/acre) only 19 percent (24 of 125 sample cones) of the pine cones were cut. This was a cool, moist fall. When the fir crop failed in 1956, during a warm, dry fall, 82 percent (40 of 49 sample cones) of a visually estimated light pine crop was removed. Intermediate to these rates was a 54 percent removal (69 of 128 samples cones) of a light (7,100 seeds/acre) pine and fir crop during average fall weather.

Many combinations of cone abundance, harvest, and squirrel population occurred between 1962 and 1972 (table 4) on the Flathead Lake study island (C. H. Halvorson, unpublished annual rept.). A medium-density (0.96 squirrels/acre) population took about half of a fair pine and fir crop (about 4 lb/acre total) in 1967 but the same density cut only about 18 percent of sample cones in the very heavy crop year of 1971 (21.7 lb total seed/acre). The seed-fall amounts (table 4) would all be adequate for regeneration, except for the 6000 fir seed/acre, but varying amounts are also taken by ground-dwelling rodents and would further reduce potential germinants. Seed abundance and the proportion of cones taken by squirrels determine how many seed reach the ground and that is variable but important information to a forest manager.

Previous studies have only reported cone crop abundance and loss without determining squirrel population densities. But even with densities accurately known it has not been possible to establish a simple linear relationship between squirrel numbers and cone loss (C. H. Halvorson unpublished). The correlations between cone crops of either the same or previous year and August and November squirrel densities have been of low order (r=0.581 to 0.381), suggesting that

factors other than crop levels determine squirrel densities and the proportion of a cone crop taken--factors such as other food availability, cone quality, predation, competition, breeding-age ratios, and weather (C. H. Halvorson unpublished). The study by Sanders (1983) on foraging by the Douglas squirrel T. douglasi in California similarly reported a lack of correlation between crop size and the proportion of white fir and Jeffrey pine cones taken. She concluded that squirrels foraged according to food encounter or energy intake rates rather than to an expectation of the cones quantity to be removed. Sanders also found evidence that squirrels with more cones on their home ranges took a significantly lower proportion of available cones than squirrels on cone-poor areas.

Seed quality is an important factor that enters into our perception and examination of cone abundance, the cone-cut, and squirrel population relationship. Douglas-fir apparently can develop full size cones without pollination or fertilization (Allen and Owens 1972). Ponderosa pine and other conifer cones also can develop normally with a low level of fertilized seed (Geo. Howe pers. comm.). Viewed from the ground in early summer, a good cone crop can be forthcoming but the promise of a crop is a familiar one to foresters. In this northern region, the year 1978 looked good for lodgepole and ponderosa pine, western larch, spruce, and fir but, except for yellow pine, the seed quality was poor in the presence of a very wet spring (John McBride pers. comm), suggesting possible pollination disruption because most species, except pine, have a one-year development cycle. Cone insects, especially Hemiptera (e.g., Leptoglossus occidentalis) are especially adept at inconspicuously damaging maturing cones that otherwise appear normal. Red squirrels, as with other seed predators, readily detect and reject poor quality food, often without having to sample it.

The total effect of squirrel clipping, from ovulate bud formation to seed germination, has been measured for ponderosa pine in Montana by Schmidt and Shearer (1971). In the first year of cone development, squirrels removed only 2 percent, the female strobili being associated with mature cone-bearing shoots ends that squirrels are prone to clip. About 44 percent of mature cones were lost the second year, the figure varying yearly as outlined earlier. A 14 percent loss of the potential cone crop was the combined effect of squirrel impact during the two-year cycle.

Squirrel Clipping of Buds and Shoots.--Red squirrels also indirectly affect cone production by their feeding on buds, clipping branch ends, and girdling in the tree crown. There are many such references for all tree species squirrels associate with (Hosley 1928; Hart 1936; Shantz-Hansen 1945; Rowe 1952; Cook 1954; Duncan 1954; Adams 1955; Lutz 1958; Walters and Soos 1961; Pulliainen and Salonen 1965).

In my experience, reproductive buds of Douglas-fir were often incorporated as food, but only when squirrels were hard-pressed for cones did they concentrate over-winter feeding on buds. In the spring of 1967 on Cedar Island, I found Douglas-fir twigs with primarily pistillate but also staminate buds eaten. Twig density over most of the island was 20-25 per 3 ft^2 (0.84 m^2) sample (C. H. Halvorson unpublished). Foresters elsewhere in the northern Rockies reported peeled basal ends of ponderosa pine shoots (see Adams 1955), needles fed on, and pine shoots blanketing the ground where squirrels lived. Specimens I examined showed typical squirrel tooth patterns. Cone crops in the region for two years prior to 1967 had been poor, and I attribute the feeding directly to lack of cones.

Terminal and lateral shoot clipping causes concern for tree form and lumber quality but

Table 4.--Cone crop harvest rate and residual seedfall in different crop years and levels of fall (Aug.-Nov.) squirrel densities. Cedar Island, Montana (C. H. Halvorson, unpublished)

Year	Squirrels per acre (ha)	Potential crop[1] P. pine	Potential crop[1] D.-fir	Cone harvest (%) P. pine	Cone harvest (%) D.-fir	Residual seed[2] P. pine	Residual seed[2] D.-fir
1962	1.1 (2.7)	5.4	5.4	71	54	15	106
1964	1.8 (4.5)	7.8	20.2	83	80	19	172
1967	0.9 (2.2)	3.6	0.3	55	53	19	6
1971	0.9 (2.2)	12.8	8.9	17	20	127	300

[1]Pounds per acre (kg/ha = 16/acre x 2.2046 ÷ 2.47).
[2]Thousands per acre (seed per ha = 1000/s ÷ 2.47).

coastal Douglas-fir saplings showed no height loss after three growing seasons where terminals had been clipped off by squirrels (Fisch and Dimock 1978). The injury was considered minimal and temporary by the authors, similar to Rowe's (1952) opinion for white spruce. Lutz (1958) observed that the club-top or tufted appearance of black spruce could be ascribed to squirrels cutting twigs in the apical aggregate of cones that characterizes the species. The bare bole section below the top functioned as a fire-break and prevented destruction of the cone crop. The effect of terminal clipping in conifers can be multiple- or fork-tops, but Hoff and Coffen (1982) saw little height difference between terminally pruned compared to unpruned single-stemmed western white pine in a seed-tree plantation. Because multiple-topped trees produced more cones and pollen, the authors recommended that leaders and terminal buds of plantation trees be pruned to maintain 1-3 stems from the 10 ft (ca. 3 m) height upwards.

Although I believe from field observation that the stag-horn branching appearance of mature and "overmature" ponderosa pine is a direct result of red squirrel feeding activity, whether for cones or survival in coneless years, it remains to be proven that shoot pruning (with accompanying apical bud removal) increases pollen and cone production in wild trees as it does for cultivated western white pine (Hoff and Coffen 1982). Pruning buds in higher plants stimulates branching and there would seem little argument that squirrels are stimulating pine branching. If more cones are produced, the squirrel benefits.

In summary, red squirrel total impact can be 14 percent of a potential ponderosa pine crop (Schmidt and Shearer 1971) but is unknown for other conifer species. Cone harvest is highly variable and crop size is not directly related to harvest rate. However, expressing the impact of squirrel cutting simply as the proportion of cones cut has little meaning to forest management without knowing crop quality and size of both the potential and residual seedfall. Even heavy loss of a bumper cone crop is likely to produce adequate seedfall for germination, but a light harvest of a poor or fair crop probably will give an inadequate seed supply. Unmeasured but real value can be assigned to squirrel cone harvest because some of the 14 percent total impact on potential crop, or 66 percent on immediate cone crop, is recoverable from caches for nursery planting (Finley 1969). Value can also be postulated for bud and shoot injury by squirrels, at least in terms of enhancing fruit production and food production structure of some tree species, but this too is unmeasured. While birds are primarily exploitive on cone crops, at least the Clark's nutcracker and pinyon jay have been shown to benefit the distribution of noncommercial, large-seeded pines in the absence of any active management programs by agencies for those species.

ANIMAL RESPONSES TO IRREGULAR CONE CROPS

Animal response to changes in prey density has been described as either numerical (Solomon 1949), or functional (Morris and others 1958). If the prey (cones) density changes and predators show increased numbers the response is termed numerical. It could include breeding effect but also the irruption phenomenon described by Bock and Lepthien (1976). Red squirrels also appear to respond numerically with increased breeding effort. A functional response occurs where access to increased prey (cones, seeds) tends to concentrate or shift foraging activities onto that prey (Morris and others 1958). The sense of "functional" has been typified mostly in forest insect outbreaks where birds actually shift from their usual foods. All seed predators show a functional shift by including more seed in their diet when it is available; some birds going back to buds and insects when the seed supply fades, or emphasizing an alternative conifer species if available. A physical response was seen in Clark's nutcrackers who weighed significantly less the winter after cone crops failed to appear in western Montana (Guintoli and Mewaldt 1978). Underweight nutcrackers in Utah in 1977 (Vander Wall and others 1981), were thought to be recent immigrants because resident birds were feeding normally on an abundant pine crop. In 1977, all cone crops in the U.S. Forest Service Northern Region were reported poor; also very spotty in 1976 (U.S.F.S. Reg. 1 Nursery Reports and R. Shearer, pers. comm.).

The stimulus effect of food (Kemper 1959) and the exploitive flocking to cone crops as they ripen is typical of crossbills (Newton 1973; Bock and Lepthien 1976); this was similarly recognized in the pinyon jay by Ligon (1978). Crossbills are also known to breed in any month, in response to cone crop abundance, but chiefly in late winter and then again late summer. Pinyon jay's second breeding in June and July (Ligon 1978) is also ascribed to food stimulus, in this case when abundant green pinyon cones are maturing. Even pine siskins and redpolls will double their breeding period in the presence of unusually abundant spruce seed crops (Newton 1973).

In summary, Nearctic redpolls, pine siskins, and crossbills all move seasonally in response to seed-ripening or in response to availability, wherever cones still hold seed. When fall conifer crops are found, the birds settle on those until the seeds are mostly eaten up or shed, then travel to the next supply. Crossbills will go into a breeding condition anytime the new supply is plentiful (e.g., Kemper 1959). The periodic mass movements ("irruptions") are also food-related but only the crossbills depend on conifer seed in cones throughout the year. When mass migrations occur, and six of the irruptive species are finches (Bock and Lepthien 1976), a combination of food shortage and large populations is believed responsible (Newton 1973). However,

Tomback (1977) suggests that a bird such as Clark's nutcracker that is intricately tied to conifer seed may only need total failure of all its conifer seed resources to irrupt, in spite of population density. The crossbill is similar enough to the nutcracker in tactical respects that it could be convergently responding the same way, or else has evolved to move and compensate for local crop failures.

Squirrel life history also contains response to cone crop abundance that may serve to drive the mechanism postulated earlier in this section, but the way this happens is still being examined (C. H. Halvorson, unpublished data). Gurnell (1983) summarized responses from the European and American literature on all tree squirrels species: "...seed availability can affect the length of the breeding season, the number of adults which produce two litters, the number of adults and yearlings which breed, and the mean litter size at birth and weaning." Not mentioned is evidence that adult squirrels, if born in high seed crop years (5 lb/acre; 5.6 kg/ha), show a median longevity of 17 months compared to 22 months for births in a poor crop year (C. H. Halvorson and Engeman 1983). I also found the breeding incidence among yearling red squirrels on Cedar Island to be 88 percent in high crop years and 51 percent in low years, a not quite significant difference and low correlation ($p=0.052$, $r=0.628$) with crop years, but crop years may not be the largest source of variation in the repeated measure ANOVA used (Halvorson unpublished; also Gurnell 1983 citation). However, an analysis of litter size difference between high and low seed abundance years showed that production of young was predictably and significantly greater if seed was plentiful ($p<0.00003$, $r=0.95$ for number of young per female). Finally, I found that in the 12-yr study some females had second litters only in the three heaviest seed crop years, 1962, 1964, and 1971 (C. H. Halvorson unpublished data), thus providing further direct evidence that squirrel populations respond to conifer seed abundance. This association has often been inferred but until now has not been previously established on a basis of both measured seed crops and accurately counted squirrel populations--a need expressed by Gurnell (1983).

SUMMARY

I have presented the names and nature of seed-eating vertebrates common to the North American West but particularly to the Inland Mountain West where most are resident species. At least 21 of the birds and mammals listed (table 1) make important use of conifer seed before it is shed from the cone. A few other bird species do so to lesser extent. The most effective predators are those who can feed habitually on closed and green cones. These include one mammal--the red squirrel; one woodpecker--the white-headed; two corvids--the pinyon jay and Clark's nutcracker; and two finches--the red- and white-winged crossbills. Except for the white-headed woodpecker whose habits are not well known, the other five have unique behaviors, morphology, and strategies that enable them to effectively exploit cone crops whenever they occur, especially in abundance. The crossbills do not store food, hence must search continuously for cones, but once found, the birds quickly transform the food energy into a reproductive thrust. The squirrel and corvids intensively gather and store food when it becomes available, using it in maintenance and later reproduction, thereby extending their predation period on seed. Corvids somewhat control competition for seeds by burying them. The squirrel eliminates most of its competitors by burying the entire closed cone and making the seed unavailable to all except other squirrels, insects, and bear. The grizzly and black bear apparently use squirrel caches when they contain whitebark and limber pine cones. The remaining predators on predispersed seed must compete for seed that is more accessible in opening cones, and these animals basically exploit an immediate food source or store portions for brief periods of days or weeks.

Those predispersal seed predators most highly adapted and effective on cone crops also return some value by being effective seed dispersers--the case of the nutcracker and pinyon jay--or, if a squirrel, by serving as a source of high quality seed for nurseries (but only if the seed didn't originate from costly seed-tree orchards). Whether benefits to trees accrue from squirrel feeding is speculative, but answerable by further study. The impact of most birds on predispersal seed is not fully assessed from the present primarily descriptive accounts, especially for the commercial conifers growing in this Inland Mountain West.

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SQUIRREL BEHAVIOR INFLUENCES QUALITY OF CONES AND SEEDS COLLECTED FROM SQUIRREL CACHES--FIELD OBSERVATIONS

Jeanne L. Pedro White and Monte D. White

ABSTRACT: Field observations were made in north-central Idaho during the 1980 through 1984 seed procurement seasons. Squirrel behavior affects the quality, location, species, maturity, and viability of seeds collected. This paper discusses some aspects of collecting seed cones for reforestation from squirrel caches. With proper care in collecting and handling cones, good quality seed can be obtained.

INTRODUCTION

The authors have observed the behavior of pine squirrels during cutting and caching of coniferous seed cones since 1980. Observations were made on the Pierce Ranger District of the Clearwater National Forest and surrounding private forest lands. This paper discusses conventional opinions about squirrel cache collection of seed cones for reforestation. Cache location, cone handling, and relative collection costs are also discussed.

CONVENTIONAL OPINION

Opinions differ on the acceptability of seed collected from squirrel caches. The most prevalent of these and our responses to them are:

Seed Maturity

Squirrels tend to harvest cones before they are mature. Response: Seeds collected from squirrel caches on the Pierce Ranger District had viability ranging from "acceptable" to "excellent", as shown in table 1. These data were obtained from germination test records of the Coeur d'Alene Nursery located in Coeur d'Alene, ID.

Seed Sources

Seed sources are uncertain. Response: Individual source trees cannot be determined with certainty when collecting cones from squirrel caches. However, while checking cone crops of potential collection sites, the authors observed that the majority of cones are to be found in the dominant and codominant trees in even-aged stands. When collecting cones, most squirrel activity was found in those trees. This is probably due to advanced maturity and relative abundance of cones found in the upper canopy. One can be relatively certain that most of the cones found in caches located within the stand were borne by those trees, although some could have been imported from adjacent stands. To ensure genetic diversity, we collected from at least seven separate cache sites within stands. Collection site desirability can thus be based on phenotypic characteristics of the larger stand components.

Squirrels Winter Food Supply

Collection from caches deprives squirrels of their winter food supply. Reponse: Squirrels collect far more cones than they can eat. If available, they will cache seeds from a variety of plants, then fail to find all of the caches. Individuals dying before winter obviously do not return to consume their caches. The authors have found old caches which have evidently remained untouched for years.

Only a portion of the squirrel caches will be found by human collectors. An example of this is that on one occasion cone pickers assigned to collect cones from the tops of felled trees didn't collect all the cones before leaving for the evening. Returning the following day, they found all the cones missing from the trees with no nearby caches to account for them.

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Table 1.--Viability of seeds collected from squirrel caches on the Pierce Ranger District, Clearwater National Forest, ID, 1980-1983

No. of Seedlots		Species	Average Viability	Range of Viability	Seedlots Below Minimum Acceptable Viability[1]
1980:	14	DF	94%	79 - 97%	0
	4	ES	91%	77 - 97%	0
	7	GF	77%	56 - 88%	0
1981:	6	LP	77%	42 - 90%	1
1982:	5	DF	95%	92 - 98%	0
1983:	1	LP	88%	-	0

[1]Acceptable minimums are: Douglas Fir (DF) = 70%; Engelman Spruce (ES) = 60%; Grand Fir (GF) = 50%; Lodgepole Pine (LP) = 70%

FINDING THE CACHES

The art of locating squirrel caches is acquired primarily through experience. Favorite cache sites include: small ground depressions (including animal tracks); cavities in and around logs, stumps, roots, and rocks; moist seeps; along the banks of small creeks; in and around structures such as fences, outbuildings, and foundations. Squirrels may enlarge the storage locations. Cones may be concealed beneath wet moss, cone scales, needles, or other debris and there may be layers of this type material between pockets of cones within the storage locations. Cache volume will range from a few cones to more than a bushel. One will not always be able to find specific types of caches or species of cones in a given area. Squirrels seem quite opportunistic in caching behavior, taking advantage of whatever storage areas are available.

Squirrels will sometimes carry cones amazing distances to be cached. On one occasion, a cone cache was found along a stream bank and the nearest seed source was 10 to 12 chains (200-240 meters) away. Many times squirrels can also be seen carrying cones across roads and skid trails. In most cases, though, cones are cached near or below the source trees.

OTHER CONSIDERATIONS

1) During years of abundance, squirrels seem to prefer true firs and Douglas-fir over pines in mixed stands. White pine cones seem to be less desirable when other species are available in collectible quantities.

2) Cone collection from squirrel caches does not result in damage to the source trees. Human collection results in tree damage. Damage ranges from incidental bark gouging and branch breakage, when using "cherry pickers" or climbing spurs, to seed tree destruction, when trees are felled prior to cone picking.

3) Cone collection costs will usually be lower if cones are obtained from caches than by more labor- and equipment-intensive means.

PROPER CONE HANDLING IS IMPORTANT

Cached cones are often wet, dirty, and/or insect-damaged. With proper on-site sorting, the collector can dispose of most undesirable cones. If cones are wet, storage of fewer cones per bag will speed drying time and prevent molding. If sound collection procedures are followed, good quality cones will usually be received at the collection station.

CONCLUSIONS

Squirrel caches are now a major source of reforestation seed on the Pierce Ranger District. Viability tests from the Coeur d'Alene Nursery on squirrel-cached seed show that mature, viable seed can be obtained in this area using the cache collection method. Caches can be found in diverse locations although, at times, they may be difficult to locate. Cache location experience combined with proper cone handling during and after collection will usually result in high-quality reforestation seed in storage.

INSECTS AND CONIFER SEED PRODUCTION IN THE INLAND MOUNTAIN WEST: A REVIEW

Gordon E. Miller

ABSTRACT: Hundreds of insects are associates of cones and seeds in the Inland Mountain West, but only a few cause economic damage. Damage by insects is one of the major impediments to seed production in Douglas-fir, spruces, ponderosa pine, western white pine, and western larch, based on the few published damage surveys from the region. Each tree species has its own complex of associated insects. Salient features of the bionomics to development of pest management systems are discussed. Major short-comings in the management of insects affecting seed production are the lack of methods for monitoring pest populations and the limited options in pest control.

INTRODUCTION

Cone and seed insects are major impediments to seed production by many conifers. Hundreds of insect species are known associates of cones in the Inland Mountain West (Keen 1958; Hedlin 1974; Kulhavy and others 1975; Hedlin and others 1980). These include insects that feed on cones and seeds, parasitoids and predators, and species of unknown feeding habit. For example, at least 67 insect species were reared from ponderosa pine cones in New Mexico in 1964-67 (Kinzer and others 1972a). Of these, 33 species fed on cones and seeds, 43 were parasitoids, 10 were predators, and 21 were of unknown feeding habit.

There have been 22 published reports of damage by cone and seed insects in the Inland Mountain West (table 1), of which 13 were general surveys for damage to various conifers while the others were concerned with specific insects. Several surveys have reported damage as the percentage of cones attacked rather than the percentage of seeds damaged. Such surveys are difficult to interpret with regard to importance of insect pests because some insect groups, e.g., scale midges, may infest a large proportion of a cone crop but, unless large numbers are present and cones or scales are killed, cause little or no seed damage. Some of the surveys have covered many sites for only one year (Allen and Ruth 1969; Ruth and others 1980), while others have covered only one site but for several years (Barnes and others 1963; Schmid and others 1981; Jenkins 1983).

The importance of cone and seed insects in the region varies among conifers (table 1). Heavy seed losses (up to 100%) have been reported in the literature for most of the tree species for which damage surveys have been conducted, i.e., Douglas-fir, ponderosa pine, western white pine, and western larch. To date losses reported in true firs and western red cedar have been less than 30%, and lodgepole pine and western hemlock have suffered very little seed loss. However, the number of site-years for which seed losses have been reported is very limited (table 1). Even in Douglas-fir, the most intensively sampled species, 81 of the 108 site-years reported were carried out in the interior of British Columbia in 1980. The lack of adequate survey makes assessment of the general importance of cone and seed insects, as well as the relative importance of individual species, in the seed production by some conifers difficult. The seed losses (table 1) may not reflect maximum potential losses for all conifers. For example, Dewey and Jenkins (1980) reported that at one site 35% of lodgepole pine cones were infested by coneworms and scale midges. Seed losses undoubtedly occurred, but were not measured, so the loss value of 0 reported in table 1 is not a true indication of potential damage. Unpublished data from the interior of British Columbia showed that more than 75% seed loss can occur in subalpine fir. Due to difficulties in damage identification for some pests, most notably seed bug (Krugman and Koerber 1967), estimates of damage by these pests are probably conservative. The need for further surveys is obvious, especially for true firs, lodgepole pine, western larch, hemlocks, and cedars.

Seed losses vary dramatically among sites and years (table 1). For example, the percentage of seed damaged in the Cariboo Region of British Columbia in 1979 varied from less than 1% to 75% for spruce at 23 sites and from 13 to 100% for Douglas-fir at 19 sites (Allen and Ruth 1979). Variation at individual sites is largely due to the irregular fluctuations in cone crop size (Mattson 1971; Forcella 1978, 1980; Miller and others 1984). When large cone crops are preceded by light or nil crops, the size of insect populations is limited so that large crops usually suffer low levels of insect damage. Where large cone crops occur closely together losses are more severe. For example, a

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Table 1.--Cone and seed insect damage reported from the Inland Mountain West and estimated seed losses

Tree species	Surveys	Number of site-years	Range seed loss (%)
Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco)	Clark and others 1963*; Dewey 1972*; Allen and Ruth 1979; Dewey and Jenkins 1979*,1980*,1982*; Ruth and others 1980; Shearer 1984	108	0-100
Grand fir (Abies grandis (Dougl.) Lindl.)	Pfister and Woolwine 1963*; Kulhavy and Schenk 1976a*, b; Dewey and Jenkins 1980*, 1982*	30	0-19
Subalpine fir (Abies lasiocarpa (Hook.) Nutt.)	Kulhavy and others 1976; Dewey and Jenkins 1982*	1	29
Western larch (Larix occidentalis Nutt.)	Dewey and Jenkins 1980*, 1982*, Ruth and others 1980; Shearer 1984	10	0-40
Spruces (Picea engelmanni Parry) P. glauca (Moench) Voss)	Hedlin 1973; Allen and Ruth 1979; Ruth and others 1980; Schmid and others 1981; Dewey and Jenkins 1982*	40	4-100
Lodgepole pine (Pinus contorta Dougl.)	Dewey and Jenkins 1979*; 1980*; Ruth and others 1980	5	0
Pinyon pine (Pinus edulis Engelm. P. monophylla Torr. & Frém.)	Forcella 1978+, 1979+	14	<5-90
Ponderosa pine (Pinus ponderosa Laws)	Kinzer and others 1972a; Dale and Schenk 1978+; Dewey and Jenkins 1979*, 1980*, 1982*; Ruth and others 1980	40	<1-100
Western white pine (Pinus monticola Dougl.)	Barnes and others 1962+; Williamson and others others 1966+; Schenk and Goyer 1967; Dewey and Jenkins 1980*, 1982*; Jenkins 1983+	16	5-98
Western red cedar (Tsuga heterophylla (Raf.) Sarg.)	Ruth and others 1980	2	0-20
Western hemlock (Thuja plicata Donn)	Ruth and others 1980	1	2

* Damage reported as percentage of cones infested only, seed losses not reported.

+ Seed loss can be estimated from the percentage of cones infested for pests that kill whole cones, e.g., Conophthorus spp.

very heavy crop of Douglas-fir cones occurred around Keremeos, British Columbia, in 1983. Most of the Douglas-fir cone moth (major pest) population remained in diapause in 1984 when a very light crop was produced. The moderate 1985 cone crop was heavily infested by the moth.

Stand density may affect seed loss and pest complex. Seed losses are higher in less dense stands in western white pine (Barnes and others 1961; Schenk and Goyer 1967). In ponderosa pine, cone beetle is more damaging in open stands whereas seed moth is more prevalent in dense stands (Dale and Schenk 1978).

Table 2.--Most damaging cone and seed insects associated with conifers in the Inland Mountain West

	Pest species no.[1]																												
Conifer	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Douglas-fir									*					*	*								*			*		*	
Grand fir					*	*		*	*			*	*			*							*						
Subalpine fir						*		*			*					*							*						
White fir					*	*		*				*	*			*	*						*						
Western larch									*																			*	*
Spruces				*																*			*				*		
Pinyon pine		*																			*			*					
Ponderosa pine	*		*						*	*								*	*			*	*		*				
Western white pine			*						*														*						
Western red cedar							*																						

[1] See table 3 for species identification.

THE PESTS

Pest Species

Only a few insect species that feed on cones and seeds of each conifer are significant pests. Based on the damage surveys, as well as other sources (Keen 1958; Hedlin 1974; Hedlin and others 1980), the important pests on conifers in the Inland Mountain West are listed in tables 2 and 3. Cone and seed insect pests represent a wide variety of insect groups, each with its own biological characteristics. Not all pests have been identified, e.g. the most damaging insects on western larch, a wooly aphid and a scale midge (Shearer 1984).

Since most pest species are host species--or genus-specific--each conifer has its own specific complex of pests. Notable exceptions are the fir coneworm, western conifer seed bug, and western budworm. The relative importance of each pest varies throughout host range. For example, spruce seed moth and spruce cone maggot occur throughout the range of spruces in the region but the moth is most damaging in the south and the maggot in the north. Ponderosa pine cone weevil occurs sporadically within the range of its host but has done significant damage at some sites (Bodenham and others 1976). The complex of pests attacking a conifer should therefore be determined at each cone and seed production site.

Insects also damage pollen cones (Dale and Schenk 1979; Hedlin and others 1980) but apparently do not reduce pollen availability.

Pest Biology

The bionomics of most of the economically important cone and seed insects are known to some extent (table 4) and are summarized elsewhere (Hedlin and others 1980). All species, except the seed bug, complete their feeding over one summer. The seed bugs feed as nymphs and young adults over one summer and as mature adults over the next summer. Aspects of biology that are significant considerations in the development of pest management systems (table 5) include stage(s) of cone attacked and damaged, methods of mate and host location, rates of survival, amount of damage per insect, location of insects at cone harvest, and capacity for prolonged diapause.

Stage(s) of cone attacked and damaged determine the timing of insecticide applications. Female cone beetles girdle and kill conelets prior to oviposition so an insecticide should be applied when females are active. Damage by seed chalcids is done by larvae but, because chalcid larvae are protected inside conelets, an insecticide should be applied at the time of oviposition to kill adult wasps. Many pests such as cone moths, cone maggots, and some seed moths, oviposit on open strobili but damage occurs after egg hatch. Against these insects, insecticides may be applied as larvicides when the conelets have closed and are turning down or as adulticides when strobili are open to receive pollen.

Knowledge of survival rates and amount of damage per insect allows for development of damage prediction systems based on counts of an insect stage, notably eggs, that occurs prior to damage. This has been done for Douglas-fir cone gall midge (Miller 1984).

Identification of cues used in mate and host location may provide tools useful in population monitoring. The utilization of pheromones in

Table 3.--Insect pests of cones and seeds in the Inland Mountain West, their common names and species number in table 2

Insect	Common name	Species number
Coleoptera: Curculionidae		
Conotrachelus neomexicanus Fall	pine cone weevil	1
Scolytidae		
Conophthorus edulis Hopkins	pinyon cone beetle	2
C. ponderosae Hopkins	ponderosa pine cone beetle	3
Diptera: Anthomyiidae		
Lasiomma anthracina (Czerny)	spruce cone maggot	4
L. abietis (Huckett)	fir cone maggot	5
Cecidomyiidae		
Dasyneura abiesemia Foote	fir seed midge	6
Mayetiola thujae (Hedlin)	western redcedar cone midge	7
Lonchaeidae		
Earomyia abietum McAlpine	fir seed maggot	8
Hemiptera: Coreidae		
Leptoglossus occidentalis Heidemann	western conifer seed bug	9
Hymenoptera: Torymidae		
Megastigmus albifrons Walker	ponderosa pine seed chalcid	10
M. lasiocarpae Crosby	-	11
M. pinus Parfitt	fir seed chalcid	12
M. rafni Hoffmeyer	-	13
M. spermotrophus Wachtl	Douglas-fir seed chalcid	14
Lepidoptera: Olethreutidae		
Barbara colfaxiana (Kearfott)	Douglas-fir cone moth	15
Barbara sp.	fir cone moth	16
Cydia bracteatana (Fernald)	fir seed moth	17
C. miscitata (Heinrich)	-	18
C. piperana (Kearfott)	ponderosa pine seedworm	19
C. strobilella (L.)	spruce seed moth	20
Eucosma bobana Kearfott	pinyon cone borer	21
E. rescissoriana Heinrich	lodgepole pine cone borer	22
Pyralidae		
Dioryctria abietivorella (Grote)	fir coneworm	23
D. albovittella (Hulst)	-	24
D. aurenticella (Grote)	ponderosa pine coneworm	25
D. pseudotsugae Munroe	-	26
D. reniculelloides Mutuura & Munroe	spruce coneworm	27
Tortricidae		
Choristoneura occidentalis Freeman	western spruce budworm	28
Unidentified species		29

mating behavior occurs in many cone and seed insects. Sex attractants have been identified for several Inland Mountain West insects, namely: Cydia piperana, Eucosma bobana, E. ponderosae, E. recissoriana, Dioryctria pseudotsugella and Barbara ulteriorana (Sartwell and others 1984), Barbara colfaxiana (Hedlin and others 1983), and Cydia strobilella (Roelofs and Brown 1982; Booij and Voerman 1984). Pests known to or suspected of using pheromones but for which sex attractants have not yet been identified include Conophthorus ponderosae and Leptoglossus occidentalis (Kinzer and others 1972b; Dale and Schenk 1979).

Table 4.--Literature on bionomics of important cone and seed insects in the Inland Mountain West

Insect	Rererence[1]
Coleoptera:	
cone weevil	Bodenham and others 1976
cone beetles	Williamson and others 1966; Kinzer and others 1970, 1972a; Dale and Schenk 1979
Diptera:	
seed midge[2]	Hedlin 1967b
seed maggots[2]	Hedlin 1967b
cone maggots	Hedlin 1973
cone midge	Hedlin 1964b
Hemiptera:	
seed bug[2]	Koerber 1963
Hymenoptera:	
seed chalcids	Hussey 1955; Hedlin 1967b; Kinzer and others 1972a
Lepidoptera:	
cone moths	Hedlin 1960; Clark and others 1963; Hedlin and Ruth 1974
budworm	McKnight 1968
seed moths	Tripp 1954; Hedlin 1967a; Kinzer and others 1972; Hedlin 1973; Dale and Schenk 1979; Schmid and others 1981
coneworms[2]	McLeod and Daviault 1963; Dale and Schenk 1979
cone borer	Ollieu and Goyer 1966

[1] In addition to the detailed accounts listed, Keen (1958) gives some information on most groups.

[2] The bionomics are well known for only a few groups, but information on these groups is particularly lacking.

Insects may be attracted to cones through host-produced volatiles (olfaction), vision, or most likely both. Pine, spruce, and larch strobili produce unique blends of volatiles (Borg-Karlson and others 1985) which insects could use in finding their host. Kinzer and others (1972b) reported that presence of ponderosa pine conelet increased attraction to the opposite sex in both male and female Conophthorus ponderosae and that females were attracted to host tree resins.

However, Mattson and others (1984) indicated that branch selection within a host tree during cone location was random in Conophthorus resinosae Hopkins, suggesting that conelet-produced volatiles are of little significance in these scolytids. The spruce cone maggot uses vision, at least in part, to locate strobili (Roques 1984). The role of host-associated stimuli in host location by cone and seed insects has yet to be determined.

Insect location at cone harvest and capacity for prolonged diapause (table 5) influence size of infestation. In seed orchards, insects which are in cones at the time of harvest are removed with the cones so that the insects must invade orchards each year for infestations to occur. Insects which are not in the cones at harvest will continually be on site. Damage will probably be greater where resident populations occur. Methods of monitoring, e.g. trap location, may differ between migrating and resident populations. Adult emergence can occur after diapause for two or more winters. This emergence can augment emergence of adults from the preceeding year's crop, resulting in greater damage (Hedlin 1964a).

The bionomics of some cone and seed pests are not well known (tables 4 and 5). The bionomics of all pests at a site must be known if pest management systems are to be effective.

PEST MANAGEMENT

Monitoring Pest Populations

Schedules for applying insecticides can be fixed (i.e., by calendar date or host phenology), flexible (i.e., when an important biological event, such as peak of oviposition is predicted to occur) or on a treat-as-necessary basis. Pest monitoring has no application in fixed-schedule spraying but is an important

Table 5.--Aspects of bionomics with implications for pest management and control

Insect	Host stage attacked	Damage by	Average number seeds damaged/insect	Location at cone harvest	Prolonged diapause
Coleoptera:					
cone weevil	2nd yr conelets	larva	?	duff	?
cone beetles	2nd yr conelets	adult	[1]3	cones on ground	yes
Diptera:					
seed midge	open strobili	larva	1	cone	yes
seed maggots	open strobili	larva	?	cone	yes
cone maggots	open strobili	larva	30	duff	yes
cone midge	open strobili	larva	?	cone	yes
Hemiptera:					
seed bug	all	adult	?	tree	no
Hymenoptera:					
seed chalcids	2nd yr conelets (pines) conelets[2] (others)	larva	1	cone	yes
Lepidoptera:					
cone moths	open strobili	larva	15	cone	yes
budworm	all	larva	?	tree	no
seed moths	2nd yr conelets (pines)	larva	12	cone	yes
	open strobili (others)	larva	14	cone	yes
coneworms	all (pines)	larva	[1]1	cone/?	no
	conelets[2] (others)	larva	?	?	no
cone borers	2nd yr conelets	larva	?	cone	?

[1] Number cones/insect

[2] 1 month after pollination

component in the latter two schedules. Cameron (1984) reviews the experiences with each approach in southern pine seed orchards. The main purpose of monitoring insect populations is the achievement of maximum control of the target pest with least amount of insecticide. Fixed schedule spraying is the least efficient way of utilizing insecticides and treating when necessary the most efficient because cone and seed insect numbers and damage vary dramatically among years and sites and control is not always warranted. Therefore, monitoring pest populations is desirable in most situations where control actions are contemplated.

Monitoring may consist of simply detecting pest presence through to quantification of pest populations and predicting damage. An effective monitoring system should allow for proper timing of insecticide applications and, when possible, for prediction of damage from the observed level of infestation.

Adult trapping with pheromone/sex attractant lures holds considerable potential for monitoring cone and seed insects. To date, none of the known attractants has been developed into a monitoring scheme. However, sex attractant-based monitoring systems have been developed for insect pests in deciduous fruit orchards (Madsen and others 1975; Madsen and Peters 1976; Vakenti and Madsen 1976) and it should be possible to develop similar systems for cone and seed insects, especially for use in seed orchards and seed production areas.

A potential problem in using sex attractant lures in seed orchards is trap placement. Because the insects must migrate into the orchards every year and mating probably takes place prior to migration, traps may need to be placed within or on the edge of nearby forest stands, which is sometimes a problem. Also, it is possible that not all cone and seed insects utilize pheromones in mating behavior. For example, the courtship behavior of Megastigmus spp. has been observed (Hussey 1955; Orr and Borden 1983) but no mention was made of pheromones. In 1984, attempts to trap M. pinus with virgin insects near Victoria, British Columbia failed.

Host attractants hold similar potential for monitoring adult populations. Host attractants have the following advantages over sex attractants: i) they should be attractive to

several species rather than being species-specific; ii) they should attract females whereas in most species males are attracted to sex attractants, and counts of females should provide a more direct estimate of potential damage; and iii) they could be used in seed orchards, thus avoiding the potential problem of trap location associated with sex attractant traps. Visual traps which simulate hosts and which also emit host volatiles are used to monitor populations of some pests in deciduous fruit orchards (Prokopy and Hauschid 1979; Reissig and Tette 1979) and such traps may be best for cone and seed insects.

Blacklight traps have been used to monitor coneworm populations in southern pine seed orchards (McLeod and Yearian 1979, 1982). They are most effective for moths; many other insects, including seed bugs (Yates 1973), are not attracted. Since these traps are not selective they can catch large numbers of many non-target lepidopteran species, resulting in difficulties in specimen identification. They are not considered practical for operational use in southern pine seed orchards (Cameron 1984).

Sampling schemes for quantifying Douglas-fir cone moth egg populations and determining the need for applications of systemic insecticide are currently being developed in British Columbia. Similar schemes are needed for populations of other pests, especially for insects which can be monitored prior to occurrence of damage, such as those which oviposit on open strobili. The current lack of monitoring schemes is a major gap in the development of pest management systems.

Control Techniques

Currently, insecticides are the only practical technique for controlling cone and seed insect populations or damage. However, in seed orchards, certain cultural practices can reduce seed losses. For instance, annual removal of insect populations in harvested cones, including unwanted cones on rootstocks or crops too small to manage for seed production, should reduce insect damage. Leaving cones in orchards allows resident insect populations to build up and results in heavier seed losses. This has happened in coastal Douglas-fir seed orchards (Miller 1984). Similarly, cone-beetle infested cones lying on the ground should be removed from orchards. Delaying reproductive bud burst through overhead misting with cold water for reducing pollen contamination may also reduce insect damage in some years (Miller 1983b). However, the effects of this technique on damage by insect pests in the Inland Mountain West have not been evaluated.

<u>Insecticides</u>. - Many contact and systemic insecticides have been tested for cone and seed insect control but only a few are effective. For example, of 26 insecticides tested on Douglas-fir cones only 11 reduced insect populations or damage by 90% or more (Miller 1980). Because of timing of sprays, contact insecticides can only be used as preventatives whereas systemic insecticides can be used after the need for insecticide application has been established, at least for insects that oviposit on open strobili. Systemic insectides have a further advantage in the number of ways that they can be applied. Systemics can be applied as sprays, injections, paint-ons, or incorporated into the soil whereas contacts can only be applied as sprays.

Insecticides effective against inportant cone and seed insects in the Inland Mountain West are listed in table 6. Significant increases in seed production after insecticide application have also been reported by Stipe and Green (1981) and Reardon and others (1984). There are few reports of insecticide efficacy against pests on conifers other than Douglas-fir, and even against some pests on Douglas-fir, such as seed bug. In Canada, azinphosmethyl and dimethoate are registered for use on Douglas-fir (Agriculture Canada 1982) and dimethoate is currently being registered for spruce cone and seed insects. In the United States, azinphosmethyl, dimethoate, Pydrin® and oxydemetonmethyl were registered for specific uses against Douglas-fir cone and seed insects (Overhulser and Sandquist 1985) and fenvalerate is registered for use on western white pine. Obviously options in pest control are limited.

Research elsewhere on cone and seed pest control may be applicable in the Inland Mountain West. For example, insecticides have been evaluated against seed bug and coneworms of southern pines (DeBarr and Nord 1978; DeBarr and Fedde 1980; Nord and DeBarr 1983; Nord and others 1984) which are related to the species in the West. These evaluations in the south provide a list of most suitable candidate insecticides for trial against western species.

Efficacy of various available application methods has not always been consistent, especially for aerial sprays and injections. Aerial sprays have sometimes been more than 90% effective (Miller and Hutcheson 1981) but have also been totally ineffective (Johnson and Winjum 1960; Johnson 1963). These "one-shot" trials have not been attempts at systematic technique development. In southern pine seed orchards, frequency of aerial applications is increasing (Barber 1984), suggesting satisfactory results are being obtained. Injections have been tested for effectiveness in reducing insect damage in Douglas-fir (Koerber and Markin 1984; Reardon and others 1984), spruce (Fogal and Lopushanski 1984) and southern pines (Merkel and DeBarr 1971), but again the results have ranged from excellent to poor. Two causes of the variation are poor uptake of the insecticide by individual trees and uneven distribution of insecticides within the tree crown (Koerber and Markin 1984). With proper timing, ground-based sprays have generally resulted in consistent effective control, provided sprays are not affected by rain (Miller

1983a; Nord and others 1984). However, ground-based sprays are limited by tree height and size of the area being treated. Incorporation of insecticides into soil has been effective in southern pine seed orchards (DeBarr 1978) and requires only one application per year, compared to several sprays for coneworm and seed bug control (Neel 1980). As with injections, level of control has varied (Nord and others 1979). Soil incorporation trials have not been reported from the West. More technique evaluation and development, as occurred in southern pine seed orchards (reviewed by Barber (1984)), is needed in our region if consistent and effective control of cone and seed insects is to be achieved in the future.

Not all application methods are equally effective against all pests. Soil incorporation of carbofuran controlled several pests on eastern white pine but not seed chalcid (DeBarr and others 1982). Likewise, timing of application for one pest may not control another. For example, injecting or spraying Douglas-fir when strobili were open or turning down controlled Douglas-fir cone gall midge and cone moth but not seed chalcid (Koerber and Markin 1984; Miller unpubl.). These points should be remembered when developing pest management systems.

The most practical method of insecticide application will vary with the type of stand to be treated. Protection of crops in forests is only practical through aerial applications because of tree size and variable terrain. Protection of seed crops on plus trees, being individual trees within forest stands, is possible through injecting insecticide and aerial spraying. In seed production areas (depending on terrain) and especially in seed orchards, all methods of application are possible. Provided the trees are not too tall and the area being treated is small, ground-based sprays or soil incorporations are likely the most cost effective. Otherwise, only aerial applications are practical. Injections are too expensive and time-consuming to be used in the treatment of whole orchards or seed production areas.

In some conifers, pest control can be relatively simple; a single application of systemic

Table 6.--Insecticides demonstrated to be 90% effective against insect pests of cones and seeds in the Inland Mountain West

Tree	Insecticide type	Insecticide name	Application method	Pest	Reference
Douglas-fir	contact	azinphosmethyl	spray	cone moth	Johnson and Winjum (1960)
			spray	coneworm	Cade (1977)
		DDT	spray	cone moth	Rudinsky (1955)
			spray	seed chalcid	Rudinsky (1955)
		lindane	spray	coneworm	Cade (1977)
		malathion	spray	seed chalcid	Stoakley (1973)
	systemic	acephate	spray	coneworm	Cade (1977)
		dicrotophos	spray	cone moth	Meso (1975)
			injection	cone moth	Meso (1975)
		carbofuran	spray	coneworm	Cade (1977)
		dimethoate	spray	cone moth	Hedlin (1966)
			spray	coneworm	Cade (1977)
			spray	seed chalcid	Hedlin (1966)
			injection	cone moth	Meso (1975)
			injection	seed chalcid	Meso (1975)
		fenitrothion	spray	seed chalcid	Hedlin (1966)
		oxydemetonmethyl	spray	cone moth	Meso (1975)
			injection	cone moth	Schenk and others (1967)
			injection	cone moth	Koerber and Markin (1984)
		phorate	spray	cone moth	Johnson and Winjum (1960)
spruce	systemic	dimethoate	spray	cone maggot	Hedlin (1973)
		oxydemetonmethyl	spray	cone maggot	Hedlin (1973)
			spray	seed moth	Hedlin (1973)
			injection	seed moth	Fogal and Lopushanski (1984)
			injection	cone maggot	Fogal and Lopushanski (1984)
		dicrotophos	injection	seed moth	Fogal and Lopushanski (1984)
			injection	cone maggot	Fogal and Lopushanski (1984)
western white pine	contact	permethrin	spray	cone beetle	Shea and others (1984)

insecticide controls both major seed pests (seed moth and cone maggot) of spruce (Hedlin 1973). In conifers attacked by only one pest species, such as western red cedar and western white pine at some sites, control should be relatively easy. In other conifers which are attacked by different pests at different stages of cone development, e.g. Douglas-fir and ponderosa pine, or by pests that initiate attacks on cones and seeds over several weeks or months, e.g. coneworms and seed bug, control of damage may be more difficult to achieve consistently and may require multiple insecticide applications.

Biological control.--The prospects for biological control appear limited, even though some insects, such as Douglas-fir cone moth (Hedlin 1960), suffer heavy losses to natural enemies because pest damage is usually completed prior to pest death caused by these mortality factors. Entomophagous fungi may provide an alternative to chemical insecticides (Timonin and others 1980) but further research is needed in evaluating these pathogens and in application techniques. Research in the southern U.S. has shown that Bacillus thuringiensis is another potential control agent for coneworms (McLeod and others 1982).

In summary, seed crops protected from one pest may suffer damage by other pests, or damage may be caused by a less important pest because no insecticide applications were made due to low levels of infestation by key pests (Cameron 1984; Miller 1984). Obviously pest management systems should be developed to include all pests associated with a conifer. Considerably more research is needed before pest management systems will be available for cone and seed pests in the Inland Mountain West.

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INSECTS DESTRUCTIVE TO PONDEROSA PINE CONE CROPS IN NORTHERN ARIZONA

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ABSTRACT: The insect damage to the 1984 ponderosa pine, Pinus ponderosa, cone and seed crop is reported. Three cone infesting insects (Dioryctria auranticella, Conophthorus ponderosae, Conotrachelus neomexicana) and two seed infesting insects (Cydia piperana, Megastigmus albifrons) were responsible for as much as 100 percent reduction in seed yield. Impact of seed and cone insect damage in 1984 is compared to previous estimates of insect damage. An economic comparison of the ponderosa pine seed value with and without insect damage is presented.

INTRODUCTION

Cone and seed insects are one of the most important biotic factors affecting seed production and thereby regeneration of ponderosa pine, Pinus ponderosa Dougl. ex Laws., in the Southwest. Studies in California (Koerber 1967), New Mexico (Kinzer and others 1972), Colorado (Bodenham 1973), and Arizona (Schmid and others 1984, unpublished manuscripts) indicate four insect species as the major damaging agents on ponderosa pine. These include the ponderosa pine coneworm (Dioryctria auranticella (Grote) (Lepidoptera: Pyralidae)), the ponderosa pine cone beetle (Conophthorus ponderosae Hopkins (Coleoptera: Scolytidae)), the ponderosa pine seedworm (Cydia piperana (Kearfott) (Lepidoptera: Olethreutidae)), and the ponderosa pine seed chalcid (Megastigmus albifrons Walker (Hymenoptera: Torymidae)). Other less prevalent cone and seed insects are the cone midge (Thomasiniana sp.), the pine cone weevil (Conotrachelus neomexicana Fall (Coleoptera: Curculionidae)), and the western conifer seed bug (Leptoglossus occidentalis Heidemann (Hemiptera: Coreidae)).

The reduction of seed yield by cone and seed insects varies by location, tree, and year. Koerber (1967) reports damage from C. piperana of 37 percent in 1963 and only 9 percent the following year. Kinzer and others (1972) report an overall reduction in seed yield of 82 percent in New Mexico, with individual trees exceeding 90 percent. Schmid and others (1984) show damage by Conophthorus ponderosae, M. albifrons, and Cydia piperana in northern Arizona varies significantly between study areas and between trees within study areas. They also report no significant differences between tree crown levels. The year to year variation in ponderosa pine cone production coupled with cone and seed insect damage makes estimates of seed yield uncertain at best.

METHODS

Five study plots were selected in fall 1984 on the Coconino and Kaibab National Forests. Each plot included 10 ponderosa pine trees ranging in height from 10 m to 15 m. Twenty live and 20 dead cones were collected from each of two crown levels (upper half and lower half). The entire live cone crop was collected from trees which produced less than 20 live cones. The collected cones were placed in labeled burlap bags and taken to the laboratory for evaluation. The number of remaining live and dead cones on each tree was counted and recorded.

Evaluation of cone and seed damage occurred in three steps. Dead cones were visually examined and the cause of mortality (Conophthorus ponderosae, Dioryctria auranticella, Conotrachelus neomexicana, or aborted) was recorded. The second step was a scale by scale dissection of all live cones. The number of sound-appearing seeds, aborted seeds, and Cydia piperana damaged seeds were recorded. Finally, all sound-appearing seeds were x-rayed and categorized as filled, unfilled, Megastigmus albifrons damaged, and other-damaged seeds.

Cone and seed insect specimens found during the study were reared to adults for species identification. Damage was then associated with the reared specimens.

All data were subjected to analysis of variance (ANOVA, α=0.05) by crown level, plot, and trees within a plot. Data were transformed where necessary to meet the assumptions of homogeneity of variance. The Student-Newman-Keuls and Least Significant Difference multiple range tests were used to determine where differences occurred.

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RESULTS

Five insect species were found to cause significant damage to the ponderosa pine cone and seed crop in 1984. A brief description of each insect species and the damage it causes is given below.

Cone Insects

Damage to cones by the ponderosa pine coneworm, Dioryctria auranticella, ranged from 19 percent to 71 percent of the total cones produced per tree. This insect species caused the heaviest damage to the cone crops in our study areas.

Dioryctria auranticella feeds on seeds and scale tissue of ponderosa pine and knobcone pine during the larval stage (Hedlin and others 1981). The larvae enter the basal portion of the cones and bore irregular shaped feeding cavities within the cone. Reddish-brown frass and webbing fill the large cavities (fig. 1). Pupation occurs within the cavity; the pupal stage lasts from 10 to 14 days. Adults emerge, mate, and lay eggs in July. Little is known of the lifecycle from July until the larvae appear in the cones the following spring. Entire cones are usually killed by D. auranticella infestation; partially killed cones become distorted and do not open.

Figure 1.--Dioryctria auranticella larva feeding on seeds and scales of ponderosa pine. Frass and webbing fill the feeding cavities.

In this study damage to cones by the ponderosa pine cone beetle, Conophthorus ponderosae, ranged from 2 percent to 19 percent per tree. The adult female beetle kills cones by severing the conductive tissue of the cone stalk (Hedlin and others 1981). A pitch tube usually marks the point where the adult enters the cone in early summer to construct a gallery and lay eggs (fig. 2). The dead cones turn brown and may remain on the tree or drop to the ground. Larvae feed randomly in the cone where they complete development in approximately one month, pupate, and emerge as adults. The adults may overwinter in the dead cones, or enter shoots or conelets where they feed and overwinter. In Arizona very few adults have been found overwintering in cones. No viable seed is produced by cones infested with C. ponderosae.

Figure 2.--A pitch tube at the base of a ponderosa pine cone marks the place where an adult Conophthorus ponderosae entered the cone.

Figure 3.--Larvae of Conotrachelus neomexicana feeding on scales and seeds of a developing ponderosa cone.

Cone damage by the pine cone weevil, Conotrachelus neomexicana, was relatively light at our study plots when compared to D. auranticella and Conophthorus ponderosae. Damage ranged from 7 percent to 14 percent of the cone crop per tree.

Larvae of C. neomexicana feed indiscriminately on the scales and seeds of developing cones (Bodenham 1973) (fig. 3). The pinkish-white to yellowish-white larvae feed for four to six weeks and, after being stimulated by rain, mature larvae chew exit holes through the outer shell of the cone and drop to the ground. They then burrow into the soil and pupate. Adults are formed in eight to 12 days but remain in the pupal cell for a few days while they darken and harden. The adults make their way to the surface, feed on shoots for a brief period, and burrow into the litter where they overwinter.

Seed Insects

Damage to seeds by the ponderosa pine seedworm, Cydia piperana, ranged from 1 percent to 11 percent of seeds per cone in this study. The

larvae consume the entire contents of each seed as they migrate from one seed to another within the cone (Hedlin and others 1981). Damaged seeds are filled with frass; seed pairs may be fused together by silk-lined tunnels of frass. Larvae burrow exit tunnels through mined seeds and then retreat to the cone axis where they overwinter (fig. 4).

Figure 4.--A mature larva of Cydia piperana in the cone axis. Larvae migrate from seed to seed, consuming the entire contents of each seed they encounter.

Pupation occurs in the spring and, after approximately two weeks, the pupae wriggle halfway through the exit hole and the adult moth emerges. One to three larvae may inhabit a single cone and may destroy a significant amount of the seed produced.

An average 53 percent of seeds which appeared to be normally developed were found to contain larvae of the ponderosa pine seed chalcid, Megastigmus albifrons, when x-rayed. Overall, 7 percent of the total seed production per cone was damaged by M. albifrons in this study.

The larvae of M. albifrons completely consume the contents of ponderosa pine seeds (Hedlin and others 1981). No external evidence of seed infestation is apparent until adults emerge in spring. Female adults oviposit through the cone scale into the immature seed. Only one larva completes development in each seed. The presence of larvae can be detected by x-raying the seed (fig. 5). Pupation occurs in the seed; adults emerge by chewing exit holes through the seed coat.

Comparison of Two Studies in Northern Arizona

Two studies of cone and seed insects in northern Arizona report the incidence of damage to ponderosa pine cone and seed production. Schmid and others (1984) reported findings for 10 locations; we report findings for five locations, three of which were studied in 1982 by Schmid and others (1984). These three plots are used for comparison of cone and seed insect damage.

Both studies report no statistically significant difference in damage between crown levels (middle

Figure 5.--Larva of Megastigmus albifrons inside a ponderosa pine seed. Seeds must be x-rayed to detect the presence of M. albifrons because no external evidence of infestation is apparent.

and lower, Schmid and others (1984), upper and lower, this study). Differences in damage caused by C. pondersae, Cydia piperana, and M. albifrons were significant between plots and among trees within plots in both studies. However, Schmid and others (1984) reported no difference in damage by D. auranticella between plots or trees within plots in 1982, while we did find these differences in 1984. Table 1 compares the incidence of D. auranticella and Conophthorus ponderosae at the US Highway 89, Deadman Flat, and Williams 345 Road plots. The incidence of D. auranticella increased dramatically in all plots from 1982 to 1984. Damage to cones by C. ponderosae decreased at the US Highway 89 and Deadman Flat plots but increased substantially at the Williams 354 Road plot. The common factor between the data is an apparent displacement of one species by the other in each year. Schmid and others (1984) did not report damage by Conotrachelus neomexicana.

A comparison of seed damage between 1982 and 1984 showed the relative effect of seed insects and environmental factors that influence viable seed production (table 2). The percentage of sound and hollow seed decreased substantially at the Deadman

Table 1.--Comparison of the percentage of dead cones killed by Dioryctria auranticella and Conophthorus ponderosae at three plots in northern Arizona

	D. auranticella		C. ponderosae	
Plot	1982[1]	1984[2]	1982	1984
US Hwy 89	1	80	39	10
Deadman Flat	1	78	15	9
Williams 354 Road	0	55	0	32
$\bar{X}$	<1	71	18	17

[1]Data for 1982 from Schmid and others (1984).
[2]Data for 1984 from this study.

Flat and Williams 354 Road plots; the US Highway 89 plot experienced a slight decline in these same categories. Schmid and others (1984) did not report aborted seed in their 1982 damage estimates. Perhaps aborted seeds were counted as hollow seeds or no obviously aborted seeds were found. Our study showed aborted seeds constituted 75 percent or more of the seed crop at all three study areas. If the percentage of aborted and hollow seeds are combined, the impact on total seed production in 1984 is substantial.

Comparison indicates a decrease in both *C. piperana* and *M. albifrons* in 1984. This decrease is probably due to the large percentage of aborted seeds which are unavailable for insect infestation. Of the seeds which appeared to be normally developed at the time of dissection, 45 to 67 percent were found to be infested with *M. albifrons* when x-rayed.

CONCLUSIONS

Damage to ponderosa pine cone and seed crops by insects is highly variable from year to year. One cause of this variation appears to be a combination of the population dynamics of the damaging insects and the size of the previous and current cone crops. If good cone crops are produced for several years and then a poor crop is produced, the insects will concentrate on the few cones and damage much of the crop. However, if several poor crops are followed by a moderate to good crop, the relatively small insect population that was supported by the poor cone crops will be dispersed and cause little damage to the large crop.

Table 3 compares the seed yield and cost per pound of seed, assuming an initial crop of 200 cones per tree. The comparison is for no insect damage and insect damage using estimates for 1982 (Schmid and others 1984) and 1984. The value of the sound seed produced per tree in 1984 is 83 times less than the value per tree if no insect damage were to occur, and 27 times less than the estimated value in 1982. The variability of the damage and value estimates between 1982 and 1984 point out the need for precise estimates of cone and seed damage prior to cone collection each year.

Table 2.--Comparison of the percentage of sound, hollow, aborted, *Cydia piperana* damaged, *Megastigmus albifrons* damaged, and other damaged seeds per cone at three locations in northern Arizona

	Sound		Hollow		Aborted		*C. piperana*		*M. albifrons*		Other	
Plot	1982[1]	1984	1982	1984	1982	1984	1982	1984	1982	1984	1982	1984
US Hwy 89	2	<1[2]	8	5	--	88	77	2	16	5	--	<1
Deadman Flat	38	<1	16	4	--	75	31	11	11	10	--	<1
Williams 354 Road	60	<1	33	7	--	84	3	1	14	6	--	<1
$\bar{X}$	33	<1	19	5	--	82	37	5	14	7	--	<1

[1] Data for 1982 from Schmid and others (1984).
[2] Percentages may not add to 100 due to rounding.

Table 3.--Comparison of the value of sound seed produced per tree for non-insect damaged and insect damaged cone crops

	No Insect Damage	Insect Damage 1982[1]	Insect Damage 1984
Initial number of cones/tree	200	200	200
% cone mortality	0	28	60
Surviving cones	200	144	80
Average number of sound seed/cone	47	21	0.9
Sound seed/tree	9,400[2]	3,024	72
Seeds/pound	11,400[3]	11,400	11,400
Pounds of sound seed/tree	0.82	0.27	0.01
Value/pound of seed	$38.00[4]	$38.00	$38.00
Value of seed/tree	$31.60	$10.26	$ 0.38

[1] Data from Schmid and others (1984).
[2] Based on U.S. Forest Service estimate of 75 percent sound seed per tree.
[3] Estimate from Schopmeyer (1974).
[4] Estimate from U.S. Forest Service.

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WESTERN SPRUCE BUDWORM IMPACT ON DOUGLAS-FIR CONE PRODUCTION

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ABSTRACT: The western spruce budworm is the most destructive pest of Douglas-fir cones in much of the Inland Mountain West. Budworm feed on Douglas-fir flowers and cones throughout their entire larval stage, sometimes destroying more than one cone. This paper discusses the general impact of budworm on cone production as determined from numerous surveys and evaluations, as well as a specific study conducted in 1983. In 1983, 772 cones on 14 trees were tagged and examined four times between early May and late August. The number of cones remaining in late August was approximately 60 percent of what was counted in May, and 21.6 percent of those were conspicuously injured by insects. This cone loss was attributable to all factors; however, the western spruce budworm was the single most damaging agent.

INTRODUCTION

For many years forest managers have recognized the western spruce budworm (*Choristoneura occidentalis* Freeman) as a severe defoliator of Douglas-fir, true fir, and spruce forests. Native to western forests, the budworm population periodically becomes epidemic over very large areas. Western spruce budworm defoliated approximately 4.2 million hectares (10.38 million acres) in the western U.S. in 1984, and another 62,000 hectares (153,202 acres) in British Columbia (Kucera and Taylor 1985).

This voracious defoliator is not widely recognized for its influence on cone and seed production. Budworm affect seed production in a number of ways. As a defoliator, they concentrate in the upper crowns of host trees. Several consecutive years of feeding will leave very thin crowns or dead tops.

Most Douglas-fir cones are produced in the upper tree crown. By topkilling potential cone-bearing trees, budworm reduce cone production. Severe defoliation may trigger a stress cone crop response in the trees, but there is uncertainty regarding the viability of seed from these cones.

Budworm reduce cone production more directly by feeding on developing flowers, cones, and reproductive buds during all stages of larval development, from emergence in the spring until pupation. Fellin (1985) reports budworm larvae become active as early as the end of April and that nearly all larvae are feeding by mid-June. Vegetative buds are usually still very tight through the month of May. But reproductive buds are swollen or may have burst by the first of May.

OBSERVATIONS

Newly emerged larvae have three food sources: mining old needles; mining tight vegetative buds; or feeding on reproductive buds or flowers. I have observed that buds and flowers are a preferred food source. While they feed freely on developing pollen buds and male flowers, the impact of this feeding has not been well evaluated. Because most conifers produce an excess of pollen, I suspect the feeding on male buds and flowers usually does insignificant damage to Douglas-fir seed production.

Budworm larvae feeding on reproductive buds, female flowers, or small conelets generally kill them by severing the conductive tissue. This results in rapid dessication and shedding, requiring the larvae to seek new feeding sites. As a result of this feeding characteristic, the budworm is particularly damaging to cones. A single larva can completely destroy one to several cones. In contrast, many of the other cone-feeding insects may destroy only a single seed or portion of a cone.

Budworm larvae are only about 1 to 2 millimeters (.04 to .08 inches) in length when newly emerged from overwintering. As a result, budworm damage is frequently overlooked or misdiagnosed. Conelets killed by budworm are often wrongly attributed to lack of pollination, abortion, or frost.

As cones grow in size, budworm feeding damage symptoms change. Fewer cones are killed outright. But various degrees of cone mining and surface feeding can be observed as the cones develop. This mining and surface feeding results in seeds being devoured, deformed cones that reduce seed recovery, and perhaps reduced seed viability.

PREVIOUS STUDIES

A number of studies provide information about budworm damage to seed production. In a cone and seed insect survey in Montana and Yellowstone National Park, Dewey (1970) found that budworm

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damaged or destroyed up to 71 percent of the Douglas-fir cones. Stipe and Hard (1980), in a light cone-crop year coupled with a large budworm population, found a peak of 8.2 early instar larvae per cone. The result was shedding of most of the developing cones and loss of the entire seed crop by the end of the season.

A survey of Idaho and Montana seed production areas revealed budworm are Douglas-fir cones' most damaging pest. Damage was greatest where the defoliator was at epidemic levels (Dewey and Jenkins 1982). Chrisman and others (1983), examining Montana Douglas-fir cone production in 12 stands with varying levels of defoliation, found that average cone production is usually higher in stands with little or no defoliation. That is, western spruce budworm infestations reduce cone production.

1983 MONTANA STUDY

A study, designed to measure the amount of Douglas-fir cone loss from flowering to cone maturity, was conducted in 1983 in a budworm-infested Douglas-fir stand near Frenchtown, MT. Fourteen flowering Douglas-fir trees, ranging from 8.5 (27.9 feet) to 13.7 meters (44.9 feet) in height, were selected for monitoring. Four cone-bearing upper crown branches were tagged on each tree. The entire cone complement per branch was counted four times between May 4 and August 31. Table 1 presents the results of cone counts at various dates.

Table 1.--Cone counts in 14 Douglas-fir trees near Frenchtown, MT, 1983

Tree number	Date				Percent loss
	5/4	6/1	7/25	8/31	
1	102	108	97	98	9
2	75	69	52	20	73
3	48	54	39	7	87
4	61	62	47	35	44
5	84	95	77	77	19
6	57	55	51	42	26
7	66	62	42	35	47
8	38	40	36	31	22
9	43	40	34	27	37
10	44	43	17	16	64
11	21	21	15	12	43
12	43	47	34	31	34
13	37	34	28	25	32
14	39	42	16	9	79
Total or Average	758	772	585	465	40

Because the conelets were only about 10 to 20 millimeters (.4 to .8 inches) long at the time of the first count, a number of them were not seen. On one tree (#5), 11 more cones were noted on the second count than on the first. As reported by Stipe and Hard (1980), considerable cone loss can occur to the small developing conelets in May. Hence more cones were apparently missed on the first count than indicated by the second count.

Agents other than budworm can cause a decline in cone numbers between May and September. While winds, hail, and rain can dislodge cones from trees, there was no evidence that these elements contributed to the reduced cone numbers during the 1983 study. Squirrels often begin cone cutting prior to August 31, but a significant amount of cone cutting had not occurred at this location prior to the final count. The cone counts in table 1 do not reflect cone conditions, just cone presence.

At the time of the last count, all cones on the survey branches were collected, taken to the laboratory, rated for insect damage, and weighed. Cones weighed an average of 4.4 grams (.16 ounces) per cone, compared to 8.8 grams (.31 ounces) for cones collected at the same time from a nearby forest where an insecticide had been used to control pests (Stipe and Dewey 1985). There was visual evidence of insect damage on 21.6 percent of the cones collected in the study.

SUMMARY AND CONCLUSIONS

Forty percent of the 772 Douglas-fir cones present on June 1 had fallen from the trees by August 31. Of the remaining 465 cones, 21.6 percent had obvious symptoms of the insect damage. Although actual counts of the pest complex were not made, the western spruce budworm was responsible for most of the damage. The study year, 1983, was a moderate to good cone-crop year, and a year with a light (nondefoliating level) budworm population.

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PROTECTION OF BLISTER RUST-RESISTANT WESTERN WHITE PINE CONES FROM INSECT DAMAGE WITH PERMETHRIN AND FENVALERATE

Michael I. Haverty and Patrick J. Shea

ABSTRACT: Production of seed from blister rust-resistant western white pine in northern Idaho has been severely reduced by the mountain pine cone beetle and the fir coneworm. In 1981 and 1984, insecticide treatments to control these insects to maximize seed production were evaluated in Idaho. At one test site, Sandpoint, 0.03 pct. permethrin significantly reduced loss of cones to the mountain pine cone beetle; however, 0.06 pct. permethrin was more cost effective. At the other test site, Moscow, the fir coneworm infested 46.6 pct. of the untreated cones, significantly more than 13.6 pct. in the single application of 0.025 pct. fenvalerate. A double application of fenvalerate increased seed yield significantly from 31.3 to 56.0 seeds/cone when compared to the untreated check. A third application of fenvalerate was apparently unnecessary.

INTRODUCTION

Western white pine (Pinus monticola Douglas) is one of the more valuable species in the northern Rocky Mountains. However, the introduction of the pathogenic fungus Cronartium ribicola Fischer to the United States from Europe in the early 1900's nearly eliminated western white pine (Haig and others 1941). To preserve this species for timber, the USDA Forest Service started a breeding program to select for resistance to this disease (Bingham 1983).

Recently, the production of blister rust-resistant seed from western white pine in seed orchards has been severely reduced in Idaho because of periodic infestations of the mountain pine cone beetle Conophthorus ponderosae Hopkins (=C. monticolae) at the Sandpoint (Idaho) Seed Orchard (Jenkins 1982; Shea and others 1984) and the fir coneworm Dioryctria abietivorella (Groté) at the Moscow (Idaho) Arboretum (Haverty and others 1985; Shea 1985). The western conifer seed bug Leptoglossus occidentalis Heidemann and the lodgepole cone moth Eucosma rescissoriana Heinrich have been observed in the Moscow Arboretum; however, we have not yet associated any significant damage with these insects.

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The life history of C. ponderosae with respect to the phenology of white pine cones has been described (Williamson and others 1966). White pine cones require about 15 months to reach maturity (Owens and Molder 1977). In early spring, as second-year cones begin to elongate, adult cone beetles emerge from overwintering sites within old cones. Female beetles initiate attack and bore into the young cones. They rapidly girdle the axis of the cone, thereby severing the conductive tissue and killing the cone. Adult females may attack up to four cones, depositing a maximum of 100 eggs. Normally, however, only 4 to 8 adults emerge from an infested cone (Jenkins 1982). The rapid attack and subsequent mortality before the cones are half-grown make successful control difficult (Furniss and Carolin 1977).

The fir coneworm is a transcontinental species that attacks cones of many conifer species. It also mines in the buds, shoots, and trunks of conifers. Its life history is variable and not well known. Apparently, in Moscow, larvae pupate in cocoons on the ground in August and September and emerge as moths in June. Eggs are laid soon after emergence, and larvae feed from June to August or September. Larvae mine the inside of cones but also crawl on the outside throughout cone development (Furniss and Carolin 1977; Hedlin and others 1980). Feeding throughout the cone development period could necessitate multiple insecticide applications.

This paper reports the results of experiments conducted in Idaho in 1981 and 1984 to evaluate single and multiple, high-volume ground applications of two insecticides--permethrin and fenvalerate--for protection of cones of blister rust-resistant western white pine. Our objective was to protect the cone crop from the major pest at two test sites (Sandpoint and Moscow) that attack cones during the second year of cone development.

MATERIALS AND METHODS

The insecticides selected were chosen on the basis of human safety and efficacy against C. ponderosae (Haverty and Wood 1981) or Dioryctria spp. and Leptoglossus corculus (Say)(Nord and others 1984).

Sandpoint-Conophthorus

The study site was the Sandpoint Seed Orchard. In 1981, the 17.3-acre (7.0-ha) orchard contained 800 grafts of 21-year-old western white pine. Trees ranged in height from approximately 15 to 45 ft (5

to 15 m). Permethrin (Pounce) was sprayed in April 1981. Ten trees between 20 and 45 ft (7 and 15 m) tall were randomly assigned to each of seven treatments. Ramets were from three clones with similar susceptibility to C. ponderosae attack (Jenkins 1982). Trees next to a previously selected tree or in a previously designated buffer zone were not used. The seven treatments consisted of an untreated check, and 0.03, 0.06 and 0.12 pct. permethrin in water applied once, the same concentrations applied again 14 days later. Trees were sprayed between 0500 and 0930 within a 2-day period with a Bean hydraulic sprayer mounted on a trailer. The sprayer was calibrated to deliver approximately 5 gallons (18.9 liters) per tree within 48 seconds. Mixing was done just before application and all trees within a treatment were treated consecutively. The order of treatment within any morning was random.

Twenty-one days following the second application and after all attacks had occurred, all cones on all trees were inspected and counted as infested vs. noninfested. Because timing is critical to protection of the cone crop, five screened cages, each with 50 infested cones collected in the orchard or from the surrounding area, were placed throughout the orchard. Spraying began 1 day after the first beetle emerged. Treatments were analyzed by pairwise tests of differences with a 2 x 2 contingency table (infested vs. noninfested vs. treatment) and a chi-square statistic at α = 0.01.

Previous work in the orchard indicated a high probability that the beetle population would be low in 1981 (Jenkins 1982). Because of concern that insufficient attacks would not allow an adequate test of the insecticide, beetles were collected elsewhere and placed throughout the orchard. Infested cones containing overwintering beetles were collected in and around Sandpoint, and held until the trees were treated. Immediately after spraying, 15 infested cones were placed under test trees (including checks) to ensure adequate attack.

Moscow-Dioryctria

The Moscow seed orchard is rectangular in shape and covers approximately 12 acres (4.9 ha) on the western edge of the University of Idaho campus. Our study area comprised the northeast quarter of the seed orchard and had approximately 340 P. monticola of cone-bearing age. Only trees with an initial cone crop of $\geq$ 20 second-year cones were used. The remainder of the seed orchard was separated from the study area by a draw at least 60 ft (20 m) wide. To protect the majority of the cone crop in the seed orchard from seed-destroying insects, this area was treated three times (once each in May, June, and July) with fenvalerate applied aerially at a rate of 0.75 lb AI/acre (0.84 kg AI/ha) delivered in 10 gallons of water (93.5 liter/ha). The draw served as a clearly visible buffer to guide the helicopter pilot so that the insecticide would not drift into the study area. Insecticide drift was monitored during each spray application with water-sensitive spray deposit cards. No drift was detected, and the study area was assumed to be free of insecticidal contamination from the adjacent control operation.

Fenvalerate (Pydrin Insecticide 2.4 EC) was diluted in water to a concentration of 0.025 pct. (wt/wt) and applied with a trailer-mounted sprayer. Mixing was done just before application. The tank mixture was applied to near the point of runoff with an FMC Bean hydraulic pumper using a hand-operated gun. Trees were sprayed in the early morning and late evening when wind was minimal to avoid contamination of adjacent trees. Between applications, spray equipment was cleaned and rinsed with Nutra Sol.

Treatments were done on three dates in 1984: 9 May, 13 June, and 18 July. Since exact phenologies of the three insect pests were unknown, the application schedules were modified after the procedure of Nord and others (1984) to be approximately 30 days apart. Pheromone traps baited with candidate E. recissoriana pheromone were distributed diagonally across the orchard at about 6 ft (2 m) above ground in trees, and inspected every other day for the appearance of adult males. The first application coincided with the first E. recissoriana catch.

The experiment was executed with a completely randomized design. Four treatments were compared: an untreated check, a single application (9 May), a double application (9 May and 13 June), and a triple application (9 May, 13 June, and 18 July). Each insecticide treatment was randomly assigned to 12 trees; 22 trees were randomly assigned to the untreated check. We selected trees spaced sufficiently apart to avoid contamination. As a result, we occasionally replaced randomly selected trees if they were too tall or too close to adjacent trees.

Before the first insecticide application, all cones on the treatment and check trees were examined and counted. Before each subsequent insecticide application, all cones were reexamined for obvious insect damage or the presence of L. occidentalis adults or nymphs. Cones with insect damage or insects present were flagged, numbered, and left on the tree. A final observation was made on 21 and 22 August. Previously infested and newly infested cones were collected and bagged separately and returned to the laboratory in Berkeley, California. The remaining cones were picked from 22 to 25 August. Cones were counted, put in separate burlap bags, and air dried.

The seed was extracted at the USDA Forest Service Coeur d'Alene Nursery, Idaho. Uncleaned seed lots from each tree were put in plastic bags and mailed to Berkeley. All seed lots were carefully cleaned. Eight groups of 100 seeds from each tree were weighed and placed in envelopes. The remaining seeds were also weighed. Seeds per tree were estimated based on the mean weight of the 800 seeds for that tree. In lots with less than 800 seeds, all seeds were counted.

The eight envelopes with 100 seeds per envelope were taped to an 8 by 10 inch (20 by 25 cm) sheet of paper and radiographed to determine percentages of empty seed, seed with a viable embryo, or seed damaged by L. occidentalis or some unknown cause. Individually collected cones damaged by insects were air dried and the seed were extracted by shaking. Seeds from each cone were counted and radiographed. Data from infested and noninfested cones were combined and used to calculate cone and seed yields for each tree.

The response variables were number of cones harvested per tree, proportion of cones infested, and number of seed per cone. Analysis of variance and analysis of covariance with the number of cones per tree as the covariate were used to detect differences between treatments at the $\alpha = 0.05$ level. Bonferroni's t-statistic (Miller 1980) was used to compare means and to maintain a $\alpha = 0.05$ for all comparisons (Jones 1984). Percentages of filled, empty, or damaged seed were also computed.

RESULTS AND DISCUSSION

Sandpoint-Conophthorus

Beetles began to emerge on 18 April, 1981, and trees were first sprayed on 19 and 20 April. Trees were resprayed on 2 May. No statistically significant difference occurred in the mean number of cones per tree by treatment (table 1). All permethrin treatments had levels of infested cones that were significantly different from the untreated controls. Additional pairwise comparisons revealed the following statistically significant relationships in percent loss of cones: 0.03 pct. once < 0.06 pct. once < 0.12 pct. once = 0.03 pct. twice < 0.06 pct. twice < 0.12 pct. twice (table 1). Percent loss of cones ranged from 75.8 pct. in the untreated controls to 1.7 pct. in the 0.12 pct. double treatment (table 1).

Moscow-Dioryctria

No statistically significant differences occurred between treatments in the number of cones harvested per tree (table 2). However, the final number of cones varied considerably between trees, and ranged from 11 to 186. Dioryctria abietivorella infested 46.6 pct. of the cones in the untreated check. This was significantly more than in any of the insecticide treatments. The proportion of infested cones among insecticide treatments did not differ significantly (table 2). Furthermore, we found no statistically significant relationship between the number of cones on a tree and the proportion of the cones which were infested.

Observations in the seed orchard in previous years indicated the presence of three potential pests of cones and seeds. Although E. recissoriana was present and captured in pheromone traps during 1984, we saw little evidence of damage by this species. Leptoglossus occidentalis also had been abundant during past years, but very few insects were observed during our test. Little, if any, cone damage was observed until 16 July 1984 (fig. 1). All damage was apparently caused by D. abietivorella. In July, less than 4.0 pct. of the cones receiving the single application of 0.025 pct. fenvalerate were damaged by coneworms, whereas ca. 25 pct. of the untreated cones were infested. By August, the proportion of damaged cones on untreated trees increased to 46.6 pct. while only 13.6 pct. of the cones on trees sprayed once and 4.1 and 5.1 pct. of the cones on trees receiving two and three sprays, respectively, were damaged (fig. 1; table 2).

Double or triple applications of 0.025 pct. fenvalerate increased seed yield significantly compared to the untreated check, that is, from 31.3 to 56.0 or 50.0 seeds/cone. The 95 pct. confidence interval for the difference in mean seeds/cone between two applications of fenvalerate and the untreated check is 24.7 ± 15.3. In other words, we are 95 pct. confident that this treatment increased seed production by at least 9.4 seeds/cone (an increase of 30.0 pct.), and possibly as much as 40.0 seeds/cone (an increase of 127.8 pct.).

Analysis of covariance showed no effect of cone crop size on number of seed per cone during 1984. All treatments also had approximately the same proportion of filled, empty, and damaged seed (table 2). This undoubtedly results from little or no feeding by L. occidentalis and random oviposition behavior of D. abietivorella.

The high cost of establishing seed orchards and the fact that these orchards are the primary, if not sole, source of resistant western white pine seed make the develoment of effective insecticide treatments an important research effort. The

Table 1.--Infested and noninfested western white pine cones, by permethrin treatment

Treatment	Cones infested	Cones noninfested	Mean cones/tree[1]	% loss of cones[1]
0.03% once	254	234	48.8a	52.0b
0.06% once	203	379	58.2a	34.8c
0.12% once	105	353	45.8a	22.9d
0.03% twice	131	478	60.9a	21.5d
0.06% twice	66	600	66.6a	9.9e
0.12% twice	8	488	45.6a	1.7f
Untreated	547	174	72.1a	75.8a

[1]Means in a column followed by the same letter are not significantly different at the $\alpha = 0.01$ level.

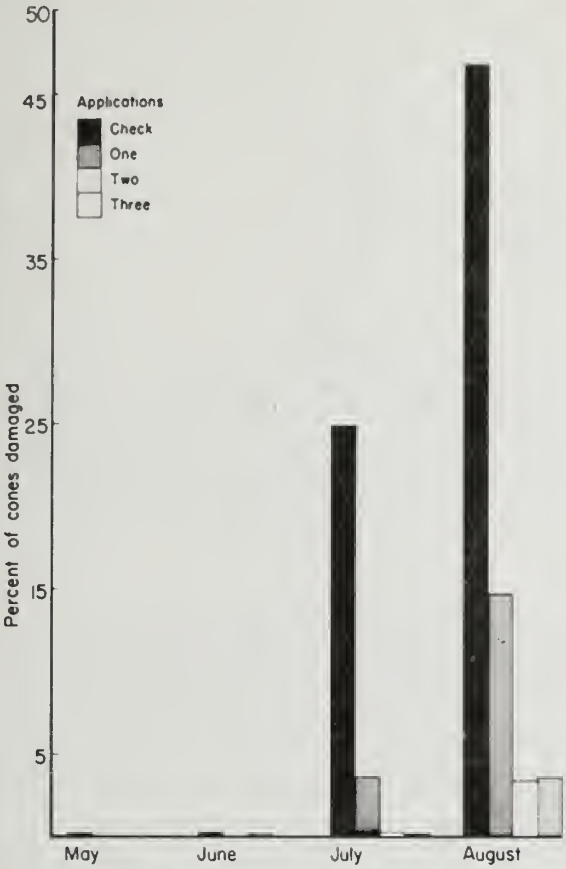

Figure 1.--Percent of western white pine cones damaged by Dioryctria abietivorella. Single applications of 0.025% fenvalerate were applied on 9 May, 13 June and 18 July.

mountain pine cone beetle C. ponderosae was the only insect of concern in the Sandpoint Seed Orchard in 1981. This insect has destroyed up to 75 pct. of the cone crop in this seed orchard. A single 0.03 pct. application of permethrin significantly reduced losses of the cone crop when compared to the untreated check (from 75.8 pct. loss to 52.0 pct. loss). Two applications of 0.12 pct. permethrin nearly eliminated cone losses. However, 0.06 pct. permethrin applied once was the most cost effective (Shea and others 1984). The fir coneworm D. abietivorella was the only insect species to cause noticeable damage in the Moscow Seed Orchard in 1984. This insect damaged almost half the cone crop on unprotected trees and reduced seed yield by about 44 pct. Two applications of 0.025 pct. fenvalerate, once in May and once in June, significantly increased seed yield. A single application in mid-June might have been sufficient to prevent coneworm damage, but was not tested. A third application in July was apparently unnecessary.

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Table 2.--Cones harvested per tree, percentage of coneworm-infested[1] cones, and seed per cone for trees treated once, twice, or three times with 0.025% fenvalerate

Treatments[2]	Cones/tree[3]	Infested Cones[3]	Seed/cone[3]	Filled seed[3]	Empty seed[3]	Damaged seed[3]
		Percent		Percent	Percent	Percent
Once	59.8 (8.8)a	13.6 (9.7)b	43.4 (9.0)ab	82.4a	17.1a	0.5a
Twice	62.1 (8.8)a	4.1 (9.7)b	56.0 (9.0)b	84.9a	14.8a	0.3a
Three times	65.8 (8.8)a	5.1 (9.7)b	50.0 (9.0)b	85.5a	13.8a	0.7a
Check	56.8 (6.5)a	46.6 (6.7)a	31.3 (6.6)a	85.9a	13.5a	0.6a

[1]Infested by Dioryctria abietivorella (Grote).

[2]Twenty-two trees were untreated and 12 trees each received either one, two, or three applications of fenvalerate.

[3]Mean (±95% confidence limit). Means in a column followed by the same letter are not significantly different by Bonferroni's t-statistic at the α = 0.05 level (Miller 1980).

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INSECT PROBLEMS AND CONTROL EFFORTS ASSOCIATED WITH SELECTED DOUGLAS-FIR PLUS TREES

William F. Johns

ABSTRACT: The Beaverhead National Forest has ground-sprayed and implanted their Douglas-fir (Pseudotsuga menziesii) plus trees in an effort to overcome effects of the western spruce budworm (Choristoneura occidentalis) on cone crops. Both methods were successful in protecting cones, but implants have several advantages over spraying.

INTRODUCTION

The tree improvement program for Douglas-fir (Pseudotsuga menziesii) calls for cones to be collected from each of the plus tree stands assigned to the Beaverhead National Forest. The seedlings from these cones will be grown in a progeny test plantation. This stage of the tree improvement program has been held up for several years due to the absence of cones in our Douglas-fir. Even without the effects of insects, good cone crops in Douglas-fir are infrequent on the Beaverhead National Forest.

Added to the natural phenology of the plant is the fact that Douglas-fir on the Forest has been heavily infested with the western spruce budworm (Choristoneura occidentalis) for a number of years. The effect of the budworm on Douglas-fir cone production is twofold: first, the budworm feeds on new foliage, lowering the tree's vigor and thereby lowering the tree's ability to produce cones. Second, the larvae feed on conelets causing cone mortality.

CONTROL EFFORTS

Around January 9, 1982, bud conditions indicated that 1982 would be a good cone year. Shortly thereafter, I contacted Jed Dewey, Regional Entomologist, Forest Service Northern Region, about what the Forest could do to overcome the negative effects of the budworm on cone production. With the help of Jed and Larry Stipe, a program was established to ground-spray our individual plus trees with a mixture of carbaryl and water.

Between June 24 and July 15, 33 stands were sprayed. The upper limit of the spray machine was about 50 feet. At the time I felt that upward drift would give us protection on to the top of the tree. I later came to feel that this was not the case. We did feel that the spray program was successful in that it allowed us to collect cones from many of our stands.

In 1984 we decided to try Acecap implants. In retrospect, that was probably a poor decision due to the poor cone crop. We had not done our homework on cone crop forecasting and were able to collect from only five of the 25 stands that were implanted. Neither method controlled cone midges.

PROJECT COSTS

Very poor cost records were kept on the spray project, but it took about 20 person-days to spray 33 stands. It took more time than desirable because our stands are scattered and I was unfamiliar with their locations.

Accurate cost records were kept on the implant operation. Fifty trees in 25 stands were implanted at a cost of $2,485. At $50 per tree, the cost seems to be excessive, but we had already collected from easy-to-reach stands with the spray operation. The biggest factor that drove up the costs was snowmobiling into the stands.

SUMMARY

To summarize, I feel that both operations were worthwhile, but the implants have considerable advantages over spraying. They are:

1. Access with a vehicle is not critical.
2. Height of the tree is not a factor.
3. Weather is not a factor.
4. Individuals do not come in contact with the chemical.
5. There is virtually no chance of environmental contamination.
6. Coverage is more consistent.

Probably the weakest part of our program during this time has been the ability to make an early estimate of our upcoming cone crop. The knowledge exists to make such an estimate; we just need to concentrate more on getting it done. In spite of our poor performance in cone forecasting, however, the use of chemicals has allowed us to reach a point where our collections are almost completed.

This spring indications were that a fair cone crop was coming so we implanted our remaining uncollected stands (18).

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IMPLANTATION AND INJECTION OF SYSTEMICS TO INCREASE SEED YIELD IN DOUGLAS-FIR

Richard C. Reardon and Larry E. Stipe

ABSTRACT: The western spruce budworm, Choristoneura occidentalis Freeman, and spruce coneworm, Dioryctria reniculelloides Mutuura and Munroe, cause widespread damage to cones of Douglas-fir, Pseudotsuga menziesii var. glauca (Beissn.) Franco. The systemic insecticide acephate injected at 4-inch (10-cm) and 6-inch (15-cm) spacings, and implanted at 4-inch spacing in Douglas-fir, increased the yield of filled seeds when compared to the checks.

INTRODUCTION

Douglas-fir, Pseudotsuga menziesii var. glauca (Beissn.) Franco, seed production areas as well as natural stands are subject to unpredictable year-to-year variation in cone crops. In the northern Rocky Mountains, western spruce budworm, Choristoneura occidentalis Freeman, is often the most serious insect pest affecting Douglas-fir cones (Dewey 1970). Other major insect pests are the Douglas-fir cone moth, Barbara colfaxiana (Kearfott); the Douglas-fir scale midge, Contarinia washingtonensis Johnson; the Douglas-fir seed chalcid, Megastigmus spermotrophus Wachtl (Dewey 1968, 1969); and the spruce coneworm, Dioryctria reniculelloides Mutuura and Munroe.

Historically, attempts to suppress populations of seed and cone insects have relied on chemical insecticides applied as foliar sprays (Dewey and others 1975; Stipe and Hard 1980; Stipe and Green 1981). This strategy is not practical for widely scattered trees in rough terrain or where adjacent areas might be sensitive to contamination. Implantation and injection of systemic chemical insecticides offer promise for individual tree protection.

Medicaps are the most widely used implantation method. Medicaps containing powdered acephate and designated as ACECAPS^R have been used to protect foliage and reduce western spruce budworm larval populations on Douglas-fir and grand fir, Abies grandis (Dougl.) (Markin 1979; Reardon and Haskett 1981; Reardon 1984a; Reardon and Barrett 1984). ACECAPS^R implanted at 4-inch (10-cm) spacing are registered for control of spruce budworms in the United States (Reardon 1984b).

Mauget systemic injector units containing oxydemeton-methyl and designated Inject-A-Cide^R are effective in reducing insect populations and increasing seed yield on Douglas-fir in California (Koerber 1978; Dale and Frank 1981). At present, mauget units with acephate are not registered for control of spruce budworms.

This paper reports a study to determine the effectiveness of Medicaps containing acephate or dimethoate and Mauget systemic injector units containing oxydemeton-methyl or acephate at two spacings in increasing the seed yield of Douglas-fir. Nutrients were also injected at 6-inch (15-cm) spacing.

MATERIALS AND METHODS

The study area of 500 acres (200 ha), about 10 miles (16 km) west of Whitehall, MT, contained open-grown Douglas-fir at ca. 5906 feet (1800 m) elevation. The trees ranged in height from 33 feet (10 m) to 64 feet (20 m) and averaged 37.1 ± 2.3 cm ($\bar{x}$ ± SD) in diameter at 4 inches (10 cm) from the soil surface. Most of the sample trees were separated by a distance of at least 20 m, numbered and randomly assigned one of eight treatments: oxydemeton-methyl injected at 10- or 15-cm intervals, nutrients injected at 15 cm, acephate injected at 10 or 15-cm, dimethoate or acephate implanted at 10 cm, and untreated checks. There were 20 sample trees per treatment except for acephate injected at the 10-(8 trees) and 15-cm (10 trees) spacings, due to a limited number of injector units.

Trees were treated on 6 and 7 April 1982, when cone buds were swollen and vegetative buds were still tight.

The powdered formulations of acephate (97 percent Orthene) and dimethoate (95 percent Dimethoate) were introduced directly into the xylem by using Medicap plastic cartridges (1 cm x 3 cm). Each acephate cartridge contained 0.9 gm active ingredient (AI) and each dimethoate cartridge contained 0.6 gm AI.

Liquid formulations of oxydemeton-methyl, as 50 percent Metasystox-R^R; acephate, as 35 percent Orthene; and nutrients, as 1 percent iron and 1 percent zinc, were injected into the xylem by using Mauget injection units. Each unit contained 1.5 g AI of oxydemeton-methyl or 1.8 g AI of acephate. The Mauget injectors were removed after 12 days.

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Four methods were used to process mature cones--air drying and shaking in bags, axial slicing, dismantling, and nursery processing; thereby, four estimates of the proportion of filled seeds per cone were obtained per treatment. Fifty mature cones were collected from the upper half of the crown from each sample tree on 30 August 1982. Twenty-five of these cones were placed in a paper bag, allowed to air dry, shaken, and the proportion of opened cones, external cone damage, and total dislodged seeds per tree were recorded. One hundred seeds from each tree were randomly selected and X-rayed to determine the proportions that were filled, hollow, and damaged by insects.

The other 25 cones from each tree were bisected longitudinally along the cone axis with cone cutters. One cut surface of each cone was examined for the number of seeds filled, hollow, and damaged by insects (Dobbs and others 1976). A subsample of 10 sliced cones per tree was dismantled by removing one scale at a time from the axis. The average number of seeds damaged by lepidopterous larvae, and numbers of scale midge and Douglas-fir cone-gall midge, *Contarinia oregonensis* Foote, per cone were recorded.

Three 1-bushel (35.2-L) samples of mature cones were collected per treatment on 1-3 September 1982, with pole pruners and by climbing the trees. Each 1 bushel of cones was collected from at least three sample trees for a treatment. At Luck Peak Nursery in Boise, Idaho, the cones were air and kiln dried, followed by tumble extraction of the seeds, seed dewinging, and air separation of filled and hollow seeds. A subsample of 300 seeds taken from the seeds determined as "filled" by air separation that were recovered from each bushel were X-rayed to determine the proportion filled, hollow, and damaged by insects. A subsample of 200 sound seeds recovered from each bushel was forwarded to the Idaho State Seed Laboratory to assess germination.

All data were analyzed by using the Games and Howell T modification for paired multiple comparisons with unequal variances (Keselman and Rogan 1978).

RESULTS

Damage by insects, as measured for mature cones processed by shaking, by axial slicing, and by dismantling, was significantly less in some treatments (table 1). The average proportion of external cone damage for each treatment, except nutrients and dimethoate, was significantly less than that for the checks. The average proportion of opened cones for each treatment provided an additional estimate of external cone damage; significant differences between treatments and checks were similar to those for external cone damage.

For the mature cones bisected longitudinally, the average insect-damaged seed per cone surface was significantly less for acephate injected at 10-cm intervals than that for each of the other treatments and checks.

For mature cones that were dismantled, the average number of seeds per cone damaged by lepidopterous larvae was significantly less for each acephate treatment than for the checks.

Table 1.--Insect damage to Douglas-fir cones on trees injected or implanted with systemic insecticides or nutrients, Montana 1982

Treatment	Shaking			Slicing		Dismantling			
	Cones processed per treatment	External cone damage (%)[1]	Cones opened (%)[1]	Cones processed per treatment	Insect-damaged seeds per cone surface[1]	Cones processed per treatment	Insect-damaged seeds per cone[1]: C. oregonensis	C. washingtonensis	Lepidopteran
		$\bar{X} \pm SE$	$\bar{X} \pm SE$		$\bar{X} \pm SE$		$\bar{X} \pm SE$	$\bar{X} \pm SE$	$\bar{X} \pm SE$
Injected									
Oxydemeton-methyl									
15 cm	500	29.7[1] ± 3.1 b	63 ± 1.0 b	494	1.8 ± 0.4 a	200	0.44 ± 0.16	0.07 ± 0.04	9.9 ± 1.2 a
10 cm	475	33.2 ± 2.9 b	54 ± 1.1 b	475	3.0 ± 0.4 a	200	0 -	0.42 ± 0.18	9.5 ± 1.4 a
Acephate									
15 cm	250	17.9 ± 4.2 b	76 ± 1.4 c	250	1.8 ± 0.3 a	100	0 -	0.65 ± 0.31	8.5 ± 1.3 b
10 cm	160	10.0 ± 3.5 c	88 ± 0.0 c	198	0.7 ± 0.2 b	80	0.90 ± 0.38	0.11 ± 0.10	3.1 ± 0.6 b
Nutrients--15 cm	500	43.2 ± 3.4 a	40 ± 1.1 a	492	2.1 ± 0.3 a	200	0.67 ± 0.23	0 -	13.3 ± 1.4 a
Implanted									
Acephate--10 cm	500	20.7 ± 3.6 b	64 ± 1.3 b	498	1.9 ± 0.3 a	200	0.15 ± 0.01	0.29 ± 0.11	4.5 ± 1.0 b
Dimethoate--10 cm	450	41.5 ± 4.1 a	48 ± 1.4 a	488	2.5 ± 0.3 a	200	0.06 ± 0.04	0 -	10.5 ± 1.1 a
Checks	500	50.7 ± 3.9 a	43 ± 11.3 a	493	3.0 ± 0.4 a	200	0.16 ± 0.08	0 -	14.6 ± 1.2 a

[1]Means in the same column followed by the same letter do not differ significantly ($P>0.05$).

Most damage to seeds and cones was caused by the western spruce budworm and spruce coneworm. Insects found in low numbers (avg. < 1 per cone) were the Douglas-fir seed chalcid, cone-scale midge and cone-gall midge.

Trees treated with dimethoate or nutrients consistently yielded greater numbers of filled seeds per cone than did the checks, but the difference was not significant (table 2). Significantly and consistently greater numbers of filled seeds per cone were detected, except for the nursery process, for oxydemeton-methyl at 15-cm intervals, and for acephate implanted and injected at 10 and 15-cm intervals, compared with the checks. Oxydemeton-methyl at the 10-cm spacing was not as consistently effective at 15-cm even though more insecticide was injected into each tree.

DISCUSSION

Oxydemeton-methyl at 15-cm intervals, acephate injected at 10- and 15-cm intervals and implanted acephate consistently and significantly increased the number of filled seeds per cone when compared with the checks. Acephate injected at 10-cm intervals was more effective than the oxydemeton-methyl treatments in protecting cones, as determined by external cone damage and percentage of opened cones, and seeds from damage by lepidopterans.

Air drying and shaking was the least time consuming of the four methods used to process mature cones. Numbers of filled seed per cone determined by this method were higher than determined by axial slicing, lower than by dismantling, and higher than by processing at the nursery.

Medicaps, with implanted acephate at 10-cm intervals and Maugets, with injected acephate at 10-cm intervals, are both effective in reducing larval densities of western spruce budworm and spruce coneworm and in increasing the number of filled seed per cone for Douglas-fir. Medicaps are registered for use against spruce budworms and do not require removal of the empty cartridge from the drilled hole. Maugets, with acephate, are not registered for use against spruce budworms, although the company has petitioned for registration. Both Medicaps and Maugets containing acephate are available at the same cost per cartridge or unit.

Table 2.--Filled Douglas-fir seed per cone (means ± SE) by treatments and cone-processing methods, Montana, 1982

Treatment	Shaking	Slicing (per cone surface)	Dismantling	Nursery Processing
Injected				
Oxydemeton-methyl				
15 cm	13.8 1/ ± 1.6 b	4.1 ± 0.5 b	15.3 ± 2.0 b	6.6 ± 1.0
10 cm	9.4 ± 1.1 a	3.2 ± 0.4 b	12.0 ± 1.3 b	7.6 ± 1.6
Acephate				
15 cm	13.6 ± 1.3 b	4.3 ± 0.7 b	11.0 ± 1.2 b	9.5 ± 1.6
10 cm	16.0 ± 2.6 b	3.3 ± 0.4 b	17.6 ± 2.9 b	8.4 ± 0.8
Nutrients--15 cm	8.0 ± 1.2 a	2.3 ± 0.3 a	9.5 ± 1.3 a	8.5 ± 0.8
Implanted				
Acephate--10 cm	14.9 ± 1.9 b	5.0 ± 0.5 b	16.9 ± 1.6 b	13.9 ± 2.9
Dimethoate--10 cm	7.0 ± 1.3 a	2.8 ± 0.4 a	10.3 ± 1.5 a	5.7 ± 1.0
Checks	5.5 ± 0.9 a	1.6 ± 0.2 a	6.0 ± 0.7 a	5.6 ± 0.7

1/ Means in the same column followed by the same letter do not differ significantly (P > 0.05).

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IMPACT OF INSECTS ON CONE/SEED PRODUCTION IN THREE BLISTER RUST-RESISTANT WESTERN WHITE PINE SEED ORCHARDS

Patrick J. Shea

ABSTRACT: Little is known about the impact of insects on production of blister rust-resistant western white pine seed. Results from sampling the only three producing seed orchards in Idaho indicate insects can severely reduce production. Further, the insect species responsible for damage differ among the various orchards. A recommendation for locating future orchards in white pine type is made based on the potential for minimizing insect-caused seed losses.

INTRODUCTION

A significant accomplishment of the breeding program for blister rust-resistant western white pine (BRR/WWP) is the establishment of three producing seed orchards in Sandpoint, Coeur d'Alene and Moscow, Idaho (Bingham 1983). Western white pine, Pinus monticola Douglas, is valued for its clean-boled form, and soft, white, easily-processed lumber. It regenerates naturally and is characterized by relatively rapid initial and continued growth. The effect and history of the introduced fungus, Cronartium ribicola Fisher, on WPP, and attempts by federal and state agencies to combat the spread of blister rust is well known (Haig and others 1941; Hepting 1971). Because of its economic importance, forest land managers of the northern Rocky Mountains have made the reestablishment of WWP to its former habitat a priority management objective.

Specific data are lacking on the effects of insects on production of BRR/WWP seed. However, insects are suspected of being responsible for substantial seed losses in all three orchards. Previous research in the Sandpoint orchard strongly indicates that Conophthorus ponderosae (=C. monticola Hopkins), the mountain pine cone beetle, is the insect primarily responsible for losses of up to 90 percent of the cones (Jenkins 1982; Bingham 1983). The situation in Moscow and Coeur d'Alene is not quite as clear. Observations by Forest Pest Management, R-1, and orchard personnel indicate that at least three insect genera are present and probably cause substantial loses. Species such as Leptoglossus occidentalis (Heidemann), western conifer seed bug, Eucosma recissoriana Heinrich, lodgepole pine cone borer, and one or more species of Dioryctria, the fir coneworms have been reared from cones. If we are to develop pest management systems for these orchards, it is critical that we accurately assess the impact of insects on BRR/WWP seed, and attempt to rank or quantify the amount of seed damaged by each insect species. The objective of this paper is to present the results of the 1984 sampling efforts.

MATERIAL AND METHODS

The three producing orchards were periodically sampled for insect damage throughout the late spring and summer of 1984. The northernmost orchard is located in Sandpoint, Idaho. It was established in 1960, and is about 17 acres (7 ha) in size. It contains 800 grafts from 13 clones and has been producing harvestable quantities of cones since 1978. In this orchard 24 trees, ranging from 20-45 ft (9 to 15 m) in height, were randomly selected for study.

The Coeur d'Alene orchard is located approximately 42 miles (67.5 km) south of Sandpoint. This orchard was established in 1960 and is about 13 acres (5 ha) in size. It is considered a low-elevation orchard and is stocked by the same families that occur in the Moscow Arboretum. This orchard is just beginning to produce harvestable quantities of cones but still requires artificial pollination. It had very few cone bearing trees in 1984 so that it was possible to examine the cones on all trees (68) that had at least three cones per tree.

The Moscow Arboretum is located about 70 miles (112.7 km) south of Coeur D'Alene and beginning in 1957 was planted with WWP seedlings that survived intense, artificial inoculation with blister rust (Hoff and Coffen 1982). This orchard covers about 23 acres (8 ha), and 22 trees 20-45 ft (9-15 m) in height were randomly selected for study. The seed produced by this orchard is shared among the 11 cooperatives in the Inland Empire Cooperative Tree Improvement Program. Only trees in the NW quadrant of the orchard were used. It is noted that this orchard is on the edge of the Palouse and is quite some distance (> 50 miles [129 km]) from any natural stands of WWP.

A hydraulic manlift was used to sample all trees. The first sample (May 18, 1984) was started one week after the second-year cones began to elongate. All cones on all sample trees were examined for insect entrance holes, presence of L. occidentalis (nymph or adult), or any other external evidence of damage. Mean numbers of cones per tree were calculated for all orchards and ANOVA (alpha =.05) was used to detect significant

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differences between orchards. Mean numbers of seeds per cone were calculated for the Moscow and Coeur d'Alene orchards only. Damaged cones were flagged and coded so that individual cones could be re-examined throughout the summer. At the end of the summer all damaged cones were removed and taken to the laboratory where they were dissected. The remaining cones on all sample trees in Coeur d'Alene and Moscow were picked, counted, put in separate labeled burlap bags, and air dried. Seeds were extracted at the USDA Forest Service Coeur d'Alene Nursery. These uncleaned seeds were put in plastic bags and shipped to Berkeley, CA for analysis. Seed lots were kept separate by tree. Eight envelopes per tree with 100 seed per envelope were radiographed to determine percentage of filled seed with viable embryo and empty seed, or seed damage by L. occidentalis, or some other unknown cause. This provided the estimate for seeds per cone and damage by L. occidentalis.

RESULTS AND DISCUSSION

In 1984, the Sandpoint Orchard had significantly more cones per tree (88.8 cones per tree) than either Moscow (56.9 cones per tree) or Coeur d'Alene (5.2 cones per tree)(alpha = .05, table 1). The small cone crop in Coeur d'Alene compared to either Moscow or Sandpoint was not unexpected since this orchard has just recently begun to produce cones. However, cone production would have been much higher than 5.2 cones per tree except that there was a high rate of cone abortion in the fall of 1983. The yield of 31.3 seeds per cone in the Moscow Arboretum is not much different than the 39 seeds per cone reported by Hoff and Coffen (1982) for this same orchard. The very low seed per cone (10.2) yield at Coeur D'Alene is thought to be due to poor pollination.

Five species of insects from three orders and four genera cause damage to BRR/WWP seeds and cones in the three orchards. When cone beetles emerge from overwintering diapause, the adult females attack maturing cones and kill them in the process. Each attacking female is later joined by an adult male. After mating she lays eggs as she feeds down the axis of the cone. One female may attack several cones (Jenkins 1982; Williamson and others 1966). Upon hatching, the larvae begin feeding throughout the cone. Both adult and immature forms of the western conifer seed bug feed on the individual maturing seeds of a wide range of conifers. The life history and habits of the seedbug on WWP are not completely known, but in natural Douglas-fir stands, there is one generation per year with ovipositing adults present from May to July and immatures from June to September (Hedlin and others 1980). This generally coincides with our observations in 1984. The fir coneworms and the lodgepole pine cone borer both attack the cones of several species of conifers. Adults oviposit on the surface of developing cones and the resulting larvae mine throughout the cone and destroy much of the seed. Preliminary results of pheromone trapping in 1984 and 1985 indicate that E. recissoriana adults begin to appear in the orchard in early June. In 1985, Dioryctria spp. were not captured in pheromone traps until two weeks after the first E. recissoriana were caught.

Table 1.--Number of trees sampled in each of three western white pine seed orchards, 1984

Orchard	N	Mean Cones/Tree ($\pm$SE)	Mean Seeds/Cone ($\pm$SE)
Moscow	22	56.9 ($\pm$6.1)	31.3 (3.16)
Coeur d'Alene	68	5.2 ($\pm$2.2)	10.2 (0.68)
Sandpoint	24	88.8 ($\pm$12.1)	NA

NA = Not assessed.

The Moscow and Coeur d'Alene orchards experience considerably more cone damage, 46.6 percent and 47.3 percent respectively, than the Sandpoint orchard (10.4 percent) (fig. 1). In Moscow virtually all the damage was attributed to the fir coneworms and perhaps the lodgepole pine cone borer (fig. 2). We have been unable to assess the amount of damage by species in this orchard. Very few seed bugs were observed in the orchard during sampling. In Coeur d'Alene, D. abietivorella was the only lepidopteran species causing damage; 37 percent of the cones were infested with larvae of this species. Cones killed by C. ponderosae were also collected from this orchard but in relatively

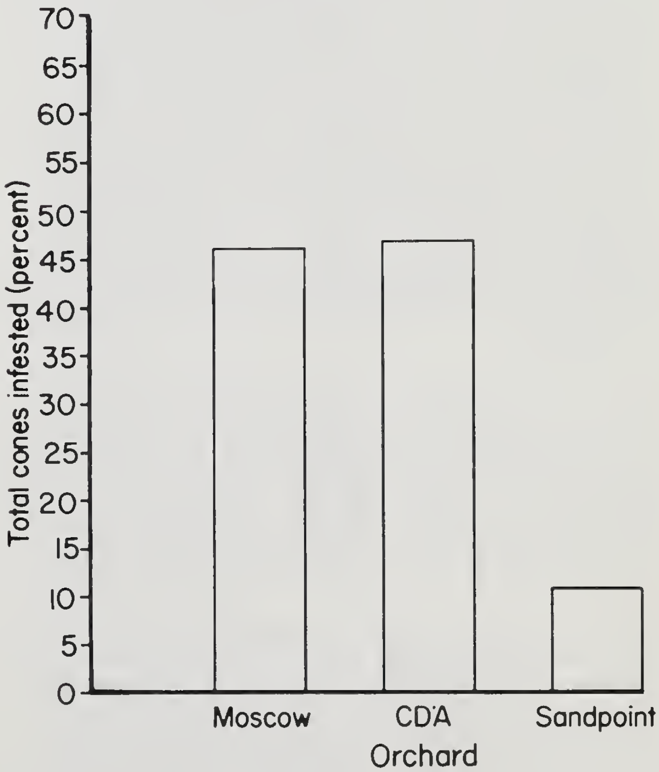

Figure 1.--Total percentage of infested cones in western white pine seed orchards, 1984.

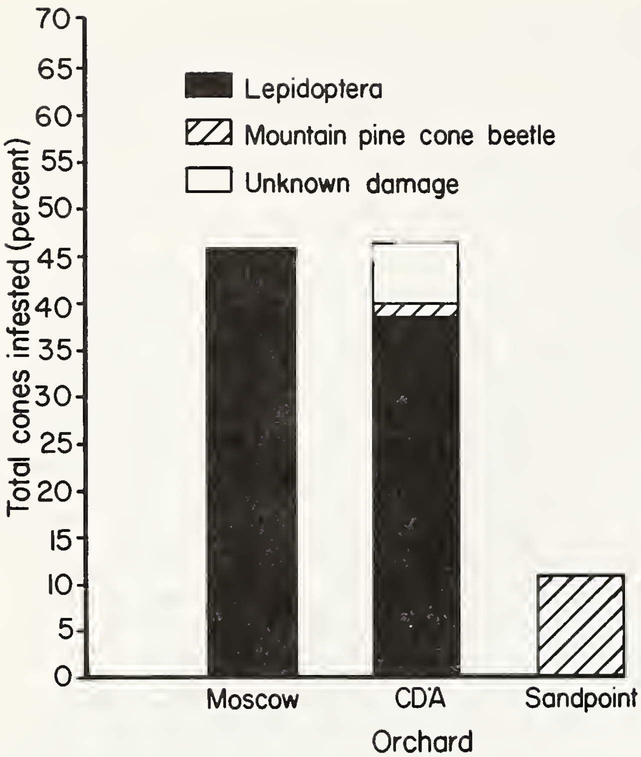

Figure 2.--Percentage of infested cones by insect group for western white pine seed orchards, 1984.

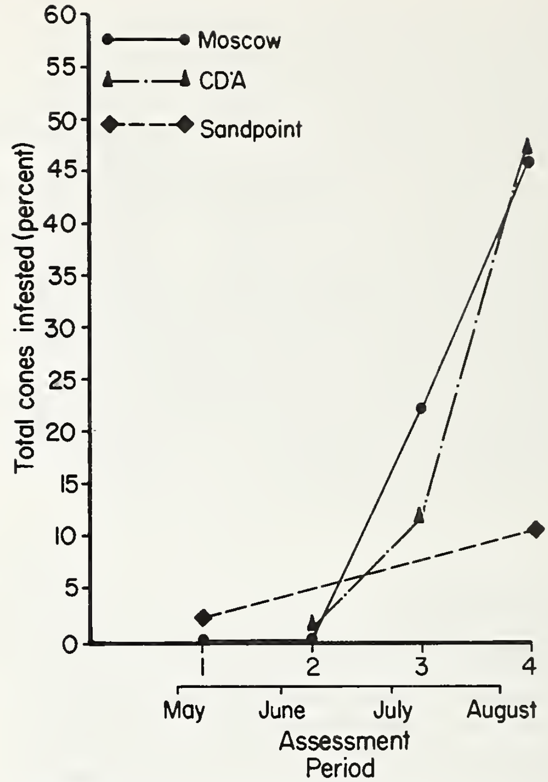

Figure 3.--Percentage of infested cones by sampling date in western white pine seed orchards, 1984.

small numbers (fig. 2). L. occidentalis populations were heaviest at Coeur d'Alene and results of radiographed seed reveal that 12 percent of the seed were destroyed by adults and immatures of this species. The full impact of L. occidentalis on production of BRR/WWP is not fully captured by x-ray analysis of seed. There is considerable suspicion that this insect may be responsible for a large share of the conelet abortion experienced in Coeur d'Alene during the fall of 1983. Studies are in place to validate whether L. occidentalis is causing conelet abortion and, if so, to what extent. C. ponderosae was the only insect species causing damage in the Sandpoint orchard (fig. 2). None of the lepidopteran species were recovered in Sandpoint and only an occassional L. occidentalis was observed.

Earliest damage occurs in the Sandpoint orchard during late April to mid-May, with the emergence of adult female cone beetles (fig. 3), but the attack period is completed by mid-June (Jenkins 1982; Shea and others 1984). At Coeur d'Alene and Moscow, visible damage begins to appear in mid-June and continues to accumulate through August (fig. 3).

Several tentative observations can be made from the 1984 impact study, all of which relate to the development and implementation of an IPM system. First, there appear to be distinct differences in the insect complex associated with the three BRR/WWP seed orchards. Second, there may be an association between the amount of damage experienced and the number of species causing damage. The more pest species in the orchard the greater the damage, e.g. Moscow vs. Sandpoint. Thirdly, in those orchards with multiple pest species the period of cone and seed vulnerability or insect attack period is longer than it is in the orchards with a single pest species such as Moscow vs. Sandpoint. If these initial observations are confirmed during the remaining two years of study, development and implementation of an IPM system in each orchard could be profoundly affected. For instance, decisions regarding management strategies to protect cones from damage in orchards with multiple pests may be quite different than in orchards with a single pest, i.e. multiple insecticide applications vs. a single application; or multiple monitoring systems vs. single monitoring system.

Lastly, note that the Sandpoint orchard is the only one of the three orchards studied that is located in white pine type; whereas, both the Moscow and Coeur d'Alene sites are located out of type. In addition, note that the three lepidopteran species and L. occidentalis can all be considered generalists as defined by Fox and Morrow (1981), that is they utilize a more diverse array of host plants than does C. ponderosae (Hedlin 1981). This suggests that contrary to the recommendation of Hoff and Coffen (1982) and Bingham (1983), it may be advantageous to locate future BRR/WWP seed orchards in white pine type. In doing so the orchard manager may only be concerned with management of a single pest as compared to a multiple pest situation and its attendant complexity.

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INFLUENCE OF DISEASES ON SEED PRODUCTION

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ABSTRACT: In this, the first of three papers on the influence of diseases on seed production, hosts, life cycles and damage, and management recommendations are given for important diseases of Inland Mountain West seed orchard trees, cones and seeds. Highlighted are Armillaria root rot, needle diseases, Inland spruce cone rust, the seed or cold fungus and Sirococcus blight.

INTRODUCTION

Although foresters and pathologists have always assumed that diseases affect seed production, it is only with the recent development of seed orchards and container nurseries that the importance of diseases of seed-producing trees and their crop have begun to be clearly defined. The high value and feasibility of protecting seed orchard trees and their cones and seeds has both necessitated and justified the development of management strategies for these diseases while container seedling production has demonstrated the importance of seed-borne pathogens in seedling disease incidence and losses. Many seed-borne problems either did not develop, were not evident, or were attributed to other causes in bareroot nurseries. Because of the increasing demand for high quality seeds we need to know how to recognize and manage diseases that affect seed orchard trees, cones and seeds and seedling pathogens such as Fusarium that are seed-borne. Not only have technological advancements increased our awareness of these various diseases, but new techniques such as the use of monoclonal antibodies have changed and improved our methods of assaying for pathogens. My goal and that of Drs. James and Mitchell in this portion of the symposium is to update and synthesize what is known about diseases affecting conifer seed production in the Inland Mountain West.

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DISEASES OF SEED ORCHARD TREES

Any tree disease likely harms seed production or quality (e.g. Schaffer and others 1983). This is true even when the disease results in increased cone production such as happens with distress cone crops on root-rot diseased trees because probably such cones yield inferior seeds. To date there is no evidence that it is worthwhile controlling diseases of seed producing trees in natural stands, including those where some silvicultural treatment has been used to stimulate or facilitate cone production, thus the following deals only with diseases of seed orchard trees. In seed orchards, tree and crop values plus easy access usually make disease management practical. Potentially, any species of seed orchard tree is susceptible to all the diseases affecting it in nature. However, the special environment of seed orchards created by fertilizing, watering, growing trees out of their natural geographic locality and other practices, may increase the risk and impact of diseases or alter their host range.

Experience indicates diseases encountered on orchard trees varies with the orchard's age. Usually the first to appear are diseases indigenous to the site or those acquired by the seedlings prior to outplanting in the orchard. For example, Armillaria root rot, Armillaria mellea (Vahl.: Fr.) Quel.), has killed 1-2% of the white spruce, Picea glauca (Moench) Voss, in an Interior B.C. orchard in the 5 years following planting, but losses are expected to decrease as inoculum, which was present in the forest that was cleared for the orchard, dies out. Western gall rust, Endocronartium harknessii (J.P. Moore) Y. Hirat., of lodgepole pine, Pinus contorta Dougl. exemplifies a disease that can be brought into a seed orchard on diseased stock. Such seedlings not only introduce the disease into the orchard, but as infection is usually on the bole, the trees are subsequently subject to wind breakage at the infection site or killing of weakened trees by secondary organisms. Presence of indigenous diseases should be one of the major selection criteria in choosing an orchard site. Although presence of a disease usually will not eliminate a potential site, it is best to reduce disease risk as much as possible before orchard establishment. When forest sites are to be used for orchards, survey and mark the root rot centers before clearing the trees, then repeatedly

root pick the area and especially the disease centers to remove pathogen-infested roots (inoculum). Alternate hosts such as those of lodgepole pine stem rusts (e.g., Indian paintbrush (Castilleja miniata Dougl. ex Hook) should be eliminated from within and adjacent to any proposed pine orchard. Alternate hosts can be prevented from re-invading the site by sowing competing grasses or other cover crops, especially perennials which can withstand repeated mowing which is detrimental to most alternate hosts. Herbicides should be used to kill alternate hosts that re-invade the seed orchard and nearby areas.

As the orchard ages, previously unencountered diseases may appear. These include foliage pathogens which are often favored by the greater volume of needles on larger trees, particularly dead and senescent needles, which may enhance pathogen buildup or survival. Undoubtedly, microclimate within the crown changes as trees become larger and this leads to other changes such as an increased volume of shade and senescent needles. Changes that may favor needle pathogens include higher humidity, longer moisture retention on needles, lower temperatures and decreased exposure to sunlight. At a Douglas-fir, Pseudotsuga menziesii (Mirb.) Franco, orchard on Vancouver Island, B.C. Meria laricis Vuill. and a newly discovered fungus, Hormonema merioides Funk, Woods & Hopkinson (Funk and others 1985), both on needles, only became evident in older orchards where cold water misting was used to retard flower development for preventing pollen contamination from outside the orchard. Defoliation was most severe on trees nearest misting stand pipes. As trees reach cone-bearing age the cultural practices change. Crown and sometimes root pruning can cause both wounds (infection courts) and stress. Cone picking can cause wounds too, especially on species such as lodgepole pine. With larger orchard trees there are the increased difficulties of detecting pathogens and applying fungicides.

Little information is available on pathogen-insect associations in Inland Mountain West seed orchards, but recently in coastal B.C. the needle cast fungus Meria has been found in wounds of a needle midge (Contarinia sp.). on Douglas-fir. This resembles a similar situation in loblolly pine, Pinus taeda L., orchards in the southern U.S.A. where the pitch canker Fusarium colonizes needle wounds made by Contarinia (Dwinell and others 1981). Pine wood nematode, Bursaphelenchus xylophilus (Steiner & Buhrer) Nickle, which is both beetle transmitted and host stress related, could occur in orchards as the result of cultural practices such as root pruning (Dwinell and Barrows-Broaddus 1983).

CONE DISEASES

Inland Spruce Cone Rust

This rust, Chrysomyxa pirolata Wint., is the most damaging cone disease in the Inland Mountain West. Cone losses of up to 60% and 67% have been recorded for natural stands in western Canada (Ziller 1974) and Utah (Nelson and Krebill 1982), respectively. Seed orchard cones appear to be equally affected as evidenced by annual losses of up to 60% in the first few years of cone production in an interior B.C. spruce orchard. Cones of all indigenous spruces are susceptible. The alternate (non-conifer) hosts are Pyrola spp. and Monesis uniflora (L.)A. Gray which are relatively small, herbaceous to woody plants. Pyrola spp. are the predominant component of the ground cover in some spruce forests. Although the fungus is holartic in distribution and occurs on alternate hosts as far south as Guatemala (Cummings 1943), cones are only affected in the northern part of its range. Nelson and Krebill (1982) give some of the possible reasons for this. In the Inland Mountain West this disease is likely to be more of a problem in the north than in the south.

The states and spores (in parentheses) in the life history of C. pirolata are spermagonial (spermatia), aecial (aeciospores), uredinial (urediniospores) and telial (teliospores). The first two occur on spruce cone scales; spermatia as a yellow-orange honeydew-type exudate in early summer and as soon as 2 weeks later, dry, yellow-orange aeciospores. Aeciospores are produced in profusion and shed from diseased cones which desiccate and open prematurely. Both the uredinial and telial states occur as yellow-orange sori on the under surface of alternate host leaves. Urediniospores spread the fungus to other alternate host plants and occur, depending upon the species of alternate host and perhaps locality, from late spring through to snowfall, but they are usually most abundant about the time of spruce cone pollination. At this time too, telia, similar in appearance to uredinia, form on the undersurface of alternate host leaves. A leaf may bear mostly uredinia, mostly telia, or both in about equal numbers. Telia produce teliospores which germinate , giving rise to basidiospores which lead to cone infection about pollination time. Information on these various states was recently published (Sutherland and others 1984).

Chrysomyxa pirolata usually becomes systemic in cones which dry out, initially becoming brownish green and later tan-brown, and open prematurely. Resinosis often accompanies these symptoms as does twisting and malformation of cone scales. Sometimes cone rust appears to be restricted to one side of the cone causing it to be slightly convex. Diseased cones should not be collected because they yield few seeds which may germinate poorly or abnormally (Nelson and Krebill 1982; Sutherland 1981A).

Cone rust loss estimates have traditionally been made by counting diseased, aeciospore-bearing cones at collection time; however, such counts underestimate cone rust losses because about one-third of the cones with spermatia in early

summer do not produce aeciospores (Sutherland and others 1984). Instead, shortly after spermatia production the cones cease development, dry out, and are often attacked by insects. In orchards where cones are readily accessible, cone rust appraisals should include comparative counts of spermatia-bearing versus aeciospore-bearing cones. Under forest conditions cone rust severity tends to be sporadic and localized. The disease depends on numerous factors including presence and phenology of the cone crop and disease on alternate hosts, weather conducive to basidiospore production, dissemination and cone infection plus synchronization of these climatic and biological phenomena. As cultural practices such as root pruning induce more regular cone crops, cone rust losses in seed orchards could exceed those in forests. Effects of other seed orchard practices are unknown, e.g., cold water misting to retard cone development might favor the disease in certain years by synchronizing cone and rust phenology. Conversely, misting could reduce losses by preventing spores from reaching susceptible cones.

Prevention of cone rust is easy, provided a seed orchard site is selected that is free of alternate hosts. The B.C. situation demonstrates this with a spruce seed orchard near Salmon Arm, where Pyrolas are abundant, regularly experiencing 15-60% cone losses while spruce orchards about 50 km south in a drier, Pyrola-free, area are free of cone rust. Although it is not known how far viable cone rust basidiospores are carried, it is suspected that disease intensity is directly proportional to closeness of the non-conifer host. Thus, practices that reduce the abundance of alternate hosts immediately around the orchard should be helpful. For example, when sufficient ground fuel was available at Salmon Arm, summer burning eliminated the Pyrolas. Summer application of paraquat or mineral oil (agricultural weed killer) was also effective against Pyrolas. Nitrogen fertilizers (NH_4SO_4 or urea) applied at forest fertilization rates in the spring and fall had no detrimental effects on P. asarifolia Michx. or P. (Orthillia) secunda L. in the second growth forest surrounding the seed orchard. Two years after fertilizer application, neither Pyrola numbers nor the ratio of healthy to diseased plants were changed, but growth of grasses and other understory plants increased dramatically. This suggested that fertilizers might be used to increase understory fuel for burning to eliminate Pyrolas. One area adjacent to the Salmon Arm orchard is pastured, but cattle avoid the abundant P. asarifolia.

Ferbam fungicide, applied to cones during the period beginning 1 week before through pollination, reduces cone rust incidence 7-10 fold (Summers and others 1985). Two sprays are recommended to compensate for differences in cone phenology. Since germination of seeds from treated cones is reduced slightly, an extremely important consideration for container nurseries, other fungicides need testing, especially systemics such as triademefon.

Other Potential Cone Diseases

Examples of other rusts that could damage cones locally include western gall rust (Byler and Platt 1972) of hard pines, spruce bud rust (McBeth 1984), and American spruce-raspberry rust (Ziller 1974). Since these pathogens are not confined to cones the potential damage is very unpredictable, especially to seed orchard cones.

SEED DISEASES

Seed or Cold Fungus

This fungus, Caloscypha fulgens (Pers.) Boud., imperfect state = Geniculodendron pyriforme Salt (Paden and others 1978) is the best known conifer seed pathogen in this area, having been isolated from seeds from Oregon and Washington (Harvey 1980), Idaho (Wicklow-Howard and Skujins 1980) and British Columbia (Sutherland 1979; Sutherland and Woods 1978). Seeds of numerous conifers are susceptible (Salt 1970; Salt and Brown 1969). The fungus occurs naturally on seeds of species with non-serotinous cones that are collected from the ground (Sutherland and Woods 1978), especially from squirrel caches (Sutherland 1979). About one-third of all spruce (Picea spp.) seedlots in B.C. are infested (Sutherland 1979). Other common hosts are seeds of Douglas-fir and true firs, Abies spp., the latter mainly because mature cones disintegrate and the pieces are collected from the forest floor. Seedlots of species such as lodgepole pine that usually have serotinous cones are disease free. Within most infested seedlots 1-5% of the seeds are diseased; however, seedlots with up to 60% affected seeds have been found. Even low numbers of diseased seeds are important because the pathogen spreads from diseased to healthy seeds at low temperatures (Epners 1964), the origin of the cold fungus name (Salt 1974), such as during seed stratification, pre-sowing storage or after sowing in cool, wet seedbeds or container cavities (Thomson and others 1983).

There are both qualitative and quantitative indicators of seed fungus infestation. Seedlots with much poorer germination when stratified are prime suspects. Losses increase as exposure to cool, wet conditions lengthens (Salt 1974). The rate of germination is important since only ungerminated seeds are susceptible, i.e., seeds are immune once germination begins (Epners 1964; Salt 1974). Seeds affected by C. fulgens are mumified and not rotted as are seeds killed by pre-emergence, damping-off fungi (Epners 1964). The seed fungus may also produce patches of indigo pigment in or around the embryo (Salt 1974; Woods and others 1982). White to whitish blue infection cushions of C. fulgens, often most abundant at the seed's distal end, may cover up to 80% of the seed coat surface (Woods

and others 1982). Quantitative determinations can be made by isolating C. fulgens from a 500-seed sample of surface sterilized (30% H_2O_2 for 30 min) seeds which are incubated at 15°C on 2% water agar (Sutherland and others 1978). The distinctive mycelium (Salt 1974), often indigo, grows from seeds within 3 weeks. Another technique (Sutherland and others 1981B) that provides either qualitative or quantitative assays for C. fulgens is based on the presence and amounts of alkaline phosphatase in infested seedlots. A major advantage of isozyme assays is that they allow use of much larger sample sizes than are physically possible with isolation-by-plating procedures.

As stated earlier, seeds acquire C. fulgens when cones contact infested forest duff. Hence, disease incidence increases with exposure time (Sutherland 1981B) and can increase further if contaminated cones are improperly stored, e.g., under cool, wet, poorly ventilated conditions. However, spread ceases if stored cones are properly air-dried (Sutherland 1981B). Seedlots originating from squirrel-cache collected cones are most likely to contain C. fulgens (Sutherland 1979). Squirrels disseminate infested cones and along with other rodents consume diseased seeds (Sullivan and others 1984). Other than disseminating the fungus, conidiospores and ascospores apparently play no obligatory role in disease development because the pathogen penetrates seeds following infection cushion formation by vegetative mycelium (Woods and others 1982). Ascospores are produced in cup-shaped fruit bodies, with a dull to bright orange hymenial layer, which occur on forest duff in early spring (Ginns 1975), often soon after snow melt.

High incidence of C. fulgens is an excellent indicator of improper cone collection or storage, or frequently both. For example, (i) cones were collected that had been on the ground for a long time, (ii) collections were from squirrel caches, and (iii) such cones were improperly stored (cool, wet, poor ventilation). The worst possible situation results from a combination of all three. When collecting cones from natural stands, hand picking them from standing trees or from slash plus proper handling afterward should greatly reduce seed fungus incidence. Since seed orchard cones are usually hand picked and properly handled afterward, the pathogen should not occur in these seeds. Cultural practices that will reduce losses when sowing infested seedlots include: (i) not stratifying the seeds or stratify them for the shortest possible period, (ii) sowing seeds quickly after stratification to avoid pre-sowing storage where the pathogen spreads, (iii) delay sowing until temperatures are warm enough to promote rapid germination and (iv) sowing as few seeds as possible per container cavity or as far apart as practical in bareroot drills. Probably the most practical recommendation is to add a suitable fungicide to the stratification water or dust the seeds with it before sowing (Gordon and others 1976; Salt 1974).

Sirococcus Blight

This disease, caused by the fungus Sirococcus strobilinus Preuss, affects conifer regeneration and forest nursery seedlings throughout the North Temperate Zone (Sutherland and others 1981A; Wall and Magasi 1976 and references cited therein; Wicker and others 1978 and references cited therein). Occasionally, minor damage occurs on older forest trees, e.g. western hemlock, Tsuga heterophylla (Raf.) Sarg.,(Funk 1972). Sirococcus blight is especially troublesome on both regeneration and nursery seedlings along those portions of the North American west coast where cooler, wet and often overcast weather favors the disease. Local hosts are spruces, e.g., white, Engelmann, Picea engelmannii Parry, Sitka, P. sitchensis (Bong.) Carr., pines such as lodgepole and yellow, Pinus ponderosa Laws., Douglas-fir and western hemlock.

In 1981 it was shown that S. strobilinus is seed-borne on spruces (Sutherland and others 1981A); subsequent observations (J.R. Sutherland and W. Lock, unpublished) indicate that it also may be seed-borne on western hemlock and yellow pine, but not lodgepole pine (Sutherland and others 1982). While the pathogen has been found on seedcoats, it normally penetrates seeds and ramifies throughout the contents (Sutherland and others 1981A) so that diseased seeds do not germinate. However, in container nurseries these dead seeds serve as inoculum for adjacent seeds which apparently acquire the fungus, germinate and emerge, then become diseased. These diseased seedlings are foci for subsequent spread of the fungus via splashing irrigation water. The situation seemingly is different in bareroot nurseries where the fungus appears to be unable to bridge the gap between diseased and healthy seeds, i.e., the latter do not acquire the pathogen before germinating. At least two factors are thought to allow the bridging in containers. Firstly the medium is probably more conducive (less microbial competition?) to Sirococcus and secondly, container seeds are sown more densely with frequently two or more seeds being sown per cavity. The latter practice also increases the likelihood of placing a diseased seed in a cavity. Sirococcus blight of bareroot seedlings can originate from inoculum in wind-blown rain (Riffle and Smith 1979), such as from nearby windbreak trees, or from inoculum on cones which fall into seedbeds (Srago 1978). Observations leading to the suspicion that S. strobilinus was seed-borne were that the disease first appeared on very young germinants of specific seedlots over several years and that the fungus is common on cones, particularly spruce.

Sirococcus blight damage and symptoms are well known on seedlings (Smith 1975; Sutherland and Van Eerden 1980) and regeneration (Wicker and

others 1978). Funk (1981) summarizes information on the pathogen such as spore size and shape. These references will be useful to persons collecting cones from natural stands. Seed orchard managers likely will not have to deal with the disease on either cones or trees, mainly because orchard cones are collected each year which removes an important source of inoculum. In nature the fungus is thought to build up on old cones that remain on trees and when these are inadvertently included in collections they are a major source of Sirococcus-infested seeds (J.R. Sutherland and T.A.D. Woods, unpublished). Another reason Sirococcus blight is unlikely to be important in seed orchards is that prolonged light stress, a major factor predisposing hosts to the pathogen (Wall and Magasi 1976), seldom occurs in orchards.

Seed-borne Sirococcus is another example of a problem created by poor cone collection practices, i.e. by including diseased cones in collections. Old cones are most likely to be diseased. This problem is difficult to overcome because late in the collection season it is extremely difficult to distinguish current year from old cones. Presence of S. strobilinus fruit bodies on cones indicates that the seeds will be infested, but laboratory confirmation is necessary because other similar-appearing fungi also fruit on cones. Attempts to remove Sirococcus-diseased seeds by repeatedly cleaning infested seedlots with air or by passage over a gravity table have been unsuccessful (J.R. Sutherland and W. Lock, unpublished). In container nurseries, benomyl or daconil fungicide drenches after sowing Sirococcus-infested spruce seedlots has produced conflicting results for disease control and the trials need repeating (G. Matthews, personal communication). In B.C., recommendations for container nurseries are to warn managers when infested seedlots are being sown so that fungicide spraying, and when practical, roguing diseased seedlings, can begin when the disease appears. Withholding watering or watering in the morning so that seedlings dry off quickly also helps alleviate damage. A disadvantage of fungicides is that they must be applied frequently to protect rapidly expanding tissues and this leads to fungicide accumulation on seedlings which concerns nursery workers and tree planters. Also, fungicides applied early in the season against Sirococcus may lead to build up of fungicide tolerance in late season pathogens such as Botrytis cinerea.

Other Cone and Seed Fungi

Besides the previously mentioned fungi and the Fusaria that Dr. James is covering in his paper, many other fungi have been reported in and on cones and seeds of local tree species (Bloomberg 1969; Harvey and Carpenter 1975; Rediske and Shea 1965; Richardson 1979; Richardson 1981; Shea 1960). Many of these are potential pathogens to cones, seeds or seedlings while others such as Heterobasidion annosum (Fr.) Bref. (Richardson 1979; Richardson 1981), which causes a butt rot of older trees, are obviously incidental. The real gray area in our knowledge concerns the role of the most common and so-called saprophytic fungi such as Penicillium and Aspergillus that have been found on cones and especially seeds. Most research on these fungi has been of a single, short-term nature and the results and interpretations to date are conflicting. Consequently few conclusions can be drawn from the literature.

Another shortfall is that since none of the studies have fulfilled Koch's Postulates it is impossible to establish a cause and effect relationship for any of these fungi. Although cones and in turn seeds apparently acquire these various fungi while still on the tree, there is no evidence that fungus development occurs until the cones have ripened and are collected. Numerous fungi can then develop on the stored cones prior to seed extraction, but mold incidence and abundance on cones appears not to subsequently affect seed quality (Bloomberg 1969). It is only after seed extraction and particularly during germination tests that molds appear (Bloomberg 1969). At least in Douglas-fir, the low percentage of healthy, non-germinable seeds indicates that the fungi and possibly bacteria are facultative parasites of low quality seeds (Bloomberg 1969). Based on our limited knowledge this seems to be true for seeds of other conifers too, e.g. reducing the abundance of molds on Abies seeds failed to increase germination (Edwards and Sutherland 1979). Examples of factors that can lower seed quality and thereby increase susceptibility to these facultative parasites include both internal and seed coat damage acquired during extraction from cones, insect damage, and probably most importantly, lack of maturity (Bloomberg 1969). The low temperatures and low moisture content of both seeds and the environment inhibit mold development in long-term storage (Holmes and Buszewicz 1958). However, in the local context nothing is known about what happens afterward during seed stratification or subsequently when seeds are stored before sowing. Present evidence indicates that incidence and abundance of so-called saprophytic fungi such as Aspergillus and Penicillium are indicators rather than the cause of poor quality seeds.

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DISEASES OF CONIFER SEEDLINGS CAUSED BY SEED-BORNE FUSARIUM SPECIES

R. L. James

ABSTRACT: The genus Fusarium includes many common soil-borne fungi that may colonize conifer seed, especially if cones are collected from the ground or squirrel caches. These fungi most commonly infect the seed coat, but can also colonize the seed embryo and endosperm. Fusarium spp. cause a wide variety of diseases, most of which affect the roots of susceptible plants. Types of diseases commonly affecting conifer seedlings in nurseries include (1) seed decay, (2) pre-emergence damping-off or germination failure, (3) postemergence damping-off, (4) topdamping-off or cotyledon blight, and (5) root diseases or late damping-off. The most common species of seed-borne fusaria include F. oxysporum, F. solani, F. moniliforme, and F. "roseum." Diseases caused by Fusarium can be reduced by seed treatments such as running water rinses, surface sterilants, and fungicides.

INTRODUCTION

Conifer seeds are storehouses of food and energy and many microorganisms have evolved mechanisms for invading and utilizing them. Many different fungi commonly infect conifer seeds. Infection frequently damages seed and also provides a means by which fungi may be transferred from one substrate or geographic location to another (Harman 1983).

Fusarium spp. are common soil-inhabiting plant pathogens (Booth 1971; Gerlach and Nirenberg 1982), which also frequently infect conifer seed (Neergaard 1977). These fungi attack a wide range of hosts and cause economically important diseases of many commercial crops, including conifer seedlings (Bloomberg 1971; Tint 1945). Fusarium spp. commonly occur within many types of soils. Populations frequently increase in cultivated soils (Booth 1971); low levels of these fungi often occur in undisturbed natural soils (Smith 1967).

Fusarium diseases of conifer seedlings have traditionally been most important in bareroot nurseries (Bloomberg 1971). Pathogen populations are often reduced in nursery soils by using fumigants such as methyl bromide and chloropicrin (Miller and Norris 1970). However, Fusarium-caused diseases sometimes occur despite soil fumigation (Cooley 1982). Investigations of diseases incited by Fusarium indicate that these fungi may be introduced into both bareroot and container nurseries on conifer seed, causing extensive losses (Cooley 1983b; Graham and Linderman 1983; James 1983a).

Although Fusarium spp. can infect conifer seed during flowering and cone formation, (Anderson and others 1980; Mason and Van Arsdel 1978; Sharma 1978), probably most infection occurs when cones or seed contact soil that harbors inoculum (James 1983c; Karrfalt 1983). Cones collected from squirrel caches often contain large populations of fungi including many pathogenic fusaria (James 1984c; James and Genz 1981; James and Genz 1982). During the seed extraction process, infection by fusaria may intensify (Salisbury 1955), resulting in both seedcoat and endosperm colonization (James 1984b; James 1984c). Diseases of seeds often increase during prolonged seed and cone storage (Bloomberg 1969; Harmon and others 1978; Harvey and Carpenter 1975). Seed colonization by pathogens can also increase during the extended seed stratification periods that are common in conifer nurseries (Bloomberg and Trelawny 1970).

TYPES OF DISEASES

Fusarium spp. cause several different kinds of diseases, the most important of which affect roots of susceptible plants (Booth 1971; Gerlach and Nirenberg 1982). Five types of diseases caused by these fungi are generally recognized on conifer seedlings. These include seed decay, pre-emergence damping-off or germination failure, postemergence damping-off, top damping-off or cotyledon blight, and root disease or late damping-off (Bloomberg 1971; Matuo and Chiba 1966).

Seed decay occurs when fungi penetrate the seedcoat, colonize it and break down internal seed contents (Bloomberg 1969). Seeds with damaged seedcoats are especially vulnerable to rapid fungal invasion (Gibson 1957; Neergaard 1977). Decayed seed may or may not be detectable from outward appearance (Bloomberg 1966). However, x-rays, which reveal hollow or partially deteriorated endosperms, can aid detection (Anderson and others 1980). Decayed seed may also be detected during water or air separation operations because of their reduced densities (James and Genz 1981; James and Genz 1982; Neergaard 1977). If decayed seed are sown, decreased germination will result and potentially pathogenic fungi are introduced into seedbeds or containers (James 1984a; Landis 1976a).

Pre-emergence damping-off occurs when the emerging radicle of germinating seed is attacked by fungi either carried on the seedcoat or present in soil (Bloomberg 1971; Graham and Linderman 1983). If the radicle is colonized by virulent fungi, decay results and no germinant emerges (Rathbun-Gravatt

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1931). Most losses to pre-emergence damping-off are never detected and are often attributed to "bad seed." Investigations of nonemergence of germlings are usually necessary to determine if pathogenic fungi are involved.

Postemergence damping-off refers to disease of newly emerged germinants. Lesions often appear at the ground line, causing infected germinants to fall over (Bloomberg 1971; Landis 1976a). Decay of the germinant follows and sporulation may occur on decayed tissues. Seed-borne fusaria may incite postemergence damping-off, resulting in reduced seedling densities (Graham and Linderman 1983; Matuo and Chiba 1966; Urosevic 1961).

Top damping-off caused by Fusarium spp. occurs as colytedon blight (Mason and van Arsdel 1978), hypocotyl rot (Brownell and Schneider 1983; Hamm, personal communication), or stem rot (Morgan 1983). Cotyledon blight is especially common on pine species that retain their seedcoats on the tips of cotyledons for extended periods after germination (Mason and van Arsdel 1978). Seed-borne fusaria move from attached seedcoats and colonize cotyledons, causing decay and eventual mortality. Hypocotyl and stem rots are caused by either natural populations of soil-borne fusaria or pathogens introduced on infected seed.

Root disease caused by Fusarium usually occurs on seedlings that are several months old. Disease results from decay of feeder roots (Pawuk and Barnett 1975); affected seedlings become slow growing and chlorotic (Landis 1976b) and may develop wilt symptoms and needle tip dieback (James 1983a; James 1984c; James 1984d). Seedling deterioration may occur either gradually or rapidly (Merrill and others 1981). The disease may cause seedling mortality or reduced seedling vigor, which adversely affect outplanting survival (LaMadeleine 1979). Seedlings may become infected during or shortly after establishment, but infecting fungi may remain inactive for several months (Bloomberg 1966). When seedlings become stressed during crown closure, periods of heat or moisture stress, or during hardening off, the infecting fungi may become active and induce disease (James 1984c; James 1984d). Another possibility is that soil-borne fusaria may become more pathogenic when seedlings are stressed. In any event, losses from root disease can continue for several months in containerized stock (James 1983c; Landis 1976b) and throughout the first and second growing seasons in bareroot stock (James 1983b; James 1983d).

SPECIES OF FUSARIUM

The most common species of Fusarium isolated from conifer seed is F. oxysporum Schlect. (Graham and Linderman 1983; James 1984b; James 1983c; James and Genz 1982). This fungus is an important seed- or soil-borne pathogen of many different plants including conifer seedlings (Booth 1971; Cooley 1983a; Gerlach and Nirenberg 1982). It is capable of causing vascular wilts (Booth 1971; Neergaard 1977) and cortical rots of seedling stems (Brownell and Schneider 1983; Morgan 1983) and roots (James 1984b; James 1983d). Although F. oxysporum exhibits a wide host range (Booth 1971; Gerlach and Nirenberg 1982) individual strains of the fungus, called formae specialis (f. sp.), usually infect only a few selective hosts (Gordon 1965; Snyder and Hansen 1940). Only one f. sp. (designated pini) is usually recognized for isolates of F. oxysporum that attack conifers (Gordon 1965).

Isolates that cause diseases of conifers are generally not thought to infect other plant species (Brownell and Schneider 1983). However, responses of different conifer species to infection by several F. oxysporum isolates have sometimes been sufficiently variable to indicate that designation of additional f. sp. (other than pini) which attack conifers might be warranted (James and Gilligan 1984; Matuo and Chiba 1966). Additional pathogenicity tests on a wide range of conifer hosts will be needed to help clarify this issue. Pathogenic isolates of F. oxysporum have been obtained from conifer seed (Graham and Linderman 1983). However, nonpathogenic isolates have also been frequently isolated. Therefore, occurrence of F. oxysporum on seed does not necessarily mean that disease will result (James 1984a; James and Genz 1982).

Another Fusarium species commonly isolated from conifer seed is F. solani (Mart.) Sacc. (James 1983a; James 1983c; James 1984a). It is a common root decay organism that is especially damaging on certain agricultural crops (Booth 1971; Gerlach and Nirenberg 1982; Neergaard 1977). The fungus is occasionally associated with diseases of conifer seedlings (Landis 1976b; Merrill and others 1981; Tint 1945). However, the pathogenic potential of seed-borne sources of this fungus is unclear for conifer seedlings.

Other species of Fusarium frequently isolated from conifer seed include F. moniliforme Sheldon and F. roseum (Lk.) Sacc. (James 1983c; James 1983e; James 1984a; James and Genz 1982). Fusarium moniliforme causes root decay in several types of plants (Booth 1971; Gerlach and Nirenberg 1982), but is infrequently associated with conifer diseases (James 1984a; Rowan 1982). Fusarium roseum is actually a complex of organisms that produce distinctive pigments in culture (Booth 1971). Members of this group are frequently isolated from conifer seed (James 1983c; James 1983e; James and Genz 1981) and less frequently from diseased seedlings (James 1983e; James 1984d; Morgan 1983). Although some of these fungi may be pathogenic (James and Gilligan 1984; Morgan 1983), most are saprophytic (Booth 1971; Gerlach and Nirenberg 1982). Seed-borne isolates of F. roseum have generally not been evaluated for their pathogenic potential.

DISEASE CONTROL

The extent of Fusarium contamination on seed varies greatly among conifer species and seedlots (James 1984a; James and Genz 1982). Differences among seedlots may be related to cone collection, storage, and seed extraction practices. Cones collected from squirrel caches often have high levels of fungal contamination. Also, cones and seed stored under

damp conditions for longer time periods are more prone to damage by fungi.

Seed treatment before sowing may reduce disease losses caused by seed-borne fusaria (Johnson and Harvey 1975; Johnson and Linton 1942). Most growers soak seed in water to condition them for sowing; some use standing water and others a running water rinse (James 1984a). If infected seed is soaked in standing water, fungal propagules can spread, causing widespread infection (James 1983e). However, placing seed under a running water rinse can reduce seedcoat contamination and does not spread infection (James 1983e; James 1984a).

Surface sterilants, such as hydrogen peroxide and sodium hypochlorite (commercial bleach), have frequently been used to reduce fungal contaminations and enhance germination of conifer seed (Advincula and others 1983; James and Genz 1981). Hydrogen peroxide usually reduces or eliminates fungal contaminants (Barnett 1976; James and Genz 1981). The effect of hydrogen peroxide on conifer seed germination has been variable. For example, some investigators (Edwards and Sutherland 1979; James 1983a) report reduced seed germination; others (Ching and Parker 1958; James and Genz 1981; Mason and van Arsdel 1978) report improved germination. Detrimental effects of H_2O_2 generally increase with chemical concentration and exposure period. Sodium hypochlorite usually reduces fungal contamination (James and Genz 1981) and sometimes enhances seed germination (Advincula and others 1983).

Several fungicides have been used for seed treatments to reduce damping-off caused by seed-borne pathogens (Mittal and Sharma 1981; Strong 1952); however, reports of fungicide toxicity to seed and germinants have limited their use (Cooley 1983a; James 1983e; Lock and others 1975). For example, use of captan has resulted in reduced seed germination (Peterson 1970), and has caused seedling injury following germination (Cayford and Waldron 1967; Lock and others 1975). Thiram, another common seed-treatment fungicide, has reduced seed germination (Dick and others 1958; Shea 1959) and caused deformed germinants (Hedderwick and Gadgil 1966). Effectiveness of seed-treatment fungicides is apparently related to dosage levels (Hamilton and Jackson 1951), activity spectrum against target organisms, development of resistant fungal strains, and persistence on seed (Sutherland and van Eerden 1980).

CONCLUSIONS

1. The genus *Fusarium* causes a wide variety of diseases of conifer seedlings.

2. Several *Fusarium* spp. have been shown to be carried both externally and internally by conifer seed.

3. The best method to reduce *Fusarium* contamination of seed is unclear, although running water rinses may be effective.

4. Seedlots of susceptible species should be bioassayed for presence of *Fusarium* after extraction to identify problem lots.

RESEARCH NEEDS

Effects of cone collection, storage, and seed handling techniques on disease caused by seed-borne fusaria need investigation. Several pertinent questions need to be answered, for example, should squirrel cache collections be permitted for susceptible species, and should cones be stored under specific conditions to reduce spread of *Fusarium*? What are the best temperatures and seed moisture levels for storage of *Fusarium*-infested seedlots? Should infested seedlots be stratified? Will stratification improve or reduce germination?

Another important research need concerns taxonomy of *F. oxysporum* strains that cause diseases of conifer seedlings. Pathogenicity tests on a wide range of conifer hosts are needed to determine host specificity characteristics of fungal strains.

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MONOCLONAL ANTIBODIES RECOGNIZING THE SEED-BORNE FUNGAL PATHOGEN *Sirococcus strobilinus*

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ABSTRACT: Hybridoma cell lines producing monoclonal antibodies (McAbs) recognizing antigens of the seed-borne conifer pathogen, *Sirococcus strobilinus* have been prepared by cell fusion techniques. Specificity of these McAbs has been ascertained in enzyme-linked immunosorbent and surface immunofluorescence assays using a panel of nonrelated commensal fungi. These McAbs will serve as reliable diagnostic probes in assaying seeds for *S. strobilinus*.

INTRODUCTION

Sirococcus shoot blight caused by the fungus, *Sirococcus strobilinus* Preuss (syn. *Ascochyta piniperda* Lindau) is an important seed-borne disease in coastal British Columbia container nurseries where it affects Sitka and white spruce (Sutherland and others 1981). The pathogenesis of *Sirococcus* blight and its confinement to specific spruce seedlots are indicative that the disease is seed-borne and recently this was confirmed by Sutherland and others (1981).

Current methods for detecting seed-borne pathogens such as *S. strobilinus* involve plating surface sterilized seeds onto nutrient media and identifying fungal outgrowth on the basis of general morphology and the production of distinctive spores. These techniques are time-consuming and insufficiently sensitive for detecting low levels of pathogens. The success of *Sirococcus* detection by these methods is low (0.5 to 3 percent) as often rapidly growing saprobes mask the slower-growing *Sirococcus*. Also, as *Sirococcus* often fails to sporulate in culture, definitive identification based on spore morphology is not always possible. However, the consequences of failure to diagnose *Sirococcus* infestation in a seedlot are often severe as nursery conditions are highly favorable to the disease. Thus, a more reliable test for this pathogen is needed. The specificity, speed and relative economy of an immunoassay would fulfill these requirements.

The primary requisite of such an immunologic test is specific antibody to serve as a probe for locating *Sirococcus strobilinus* components (antigens) in or on seeds. Techniques devised by Köhler and Milstein (Köhler and Milstein 1975; Milstein 1980) permit the isolation of cells which produce antibodies of unique specificities (called monoclonal antibodies). In this procedure, antibody-forming cells taken from the spleen of a mouse that has been immunized with antigen are fused to cancerous myeloma cells to form new cells (called hybridomas) which have the ability to live indefinitely in culture and to produce and to secrete into the culture fluids monoclonal antibodies (McAbs) directed to the antigen.

This paper describes the derivation, by cell fusion techniques, of hybridoma cell lines which produce McAbs recognizing antigens of *S. strobilinus*. The McAbs recognize antigens from several *S. strobilinus* isolates obtained from diverse host species and tissues but do not react with other nonrelated seed-associated fungi when tested in enzyme-linked immunosorbent (ELISA) or by indirect surface immunofluorescence (IFA) assays and thus will be useful diagnostic probes for *Sirococcus* in seeds and other tissues.

MATERIALS AND METHODS

Fungal Isolation and Culture

Axenic cultures of *Sirococcus strobilinus* and 10 other saprophytic fungi isolated from surface-sterilized (Sutherland and others 1978) seeds obtained from an Engelmann spruce (*Picea engelmanni* Parry) seedlot were prepared as previously described (Sutherland and others 1981). Fungi used for immunizing mice or for the preparation of soluble antigens were grown in 1.25% malt extract broth (MB) containing trace amounts of B, Cu, Fe, Mn, Mo and Zn (Vézina and others 1965).

Preparation of Fungal Antigens

Antigens for immunizing mice and for testing McAbs were prepared as follows. Mycelium from axenic cultures of *S. strobilinus* and commensal fungi, grown in MB, was separated from the culture medium, washed with 100 mL of distilled water by vacuum filtration and used directly or frozen at -20°C.

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Total antigens.--Mycelium (5-10 g) was homogenized immediately in a volume of 3-4 mL of phosphate buffered saline (PBS, pH 7.4 containing 10 mM Na and K phosphates, 3 mM KCl and 140 mM NaCl) in a glass homogenizer, then dried for 24 hr at 40°C in glass Petri dishes. The dried mycelium was scraped from the Petri dish, ground into a fine powder and stored at 4°C.

Soluble antigens.--Five to 10 g of frozen mycelium was suspended in 20 mL of extraction buffer (50 mM NH_4HCO_3/2% w/v polyvinylpyrrolidone) and homogenized for 2 min at maximum speed in a polytron homogenizer (Type PT 20-OD, Kinematica, Lucerne, Switzerland). The disrupted mycelium was held at 0°C for 1 hr, rehomogenized, then centrifuged for 20 min at 600 x g. The supernatant was saved and the pellet re-extracted twice with 15 mL of extraction buffer. Supernatants from all extractions were pooled, cleared by centrifugation at 12000 x g and stored -20°C. Protein concentrations were determined as described by Lowry and others (1951).

Secreted antigens.--Antigens secreted into culture fluids were prepared by mixing two volumes of 95% ethanol with one volume of filtered culture fluids. Precipitation was allowed to occur for 24-48 hours at 4°C then the mixture was centrifuged for 30 min at 10000 x g and the pellet redissolved in 10-20 mL of distilled water and stored at -20°C.

Animals

BALB/c mice were obtained from Charles River (Canada) Inc., St. Constant, Que, or bred from parental stock purchased from the same source. Both male and female mice, aged 6-12 weeks were used.

Immunization of Animals

Mice were immunized by intraperitoneal (i.p.) injection of 5 mg of air-dried mycelium emulsified with Freund's complete adjuvant in a volume of 0.2 mL/animal and challenged five times at 4-6 week intervals by i.p. injection of 1 mg of mycelium in Freund's incomplete adjuvant in the same volume. Three days before cell fusion mice were given 0.1 mL of *S. strobilinus* soluble antigens intravenously.

Sera from mice hyperimmunized with *S. strobilinus* dried mycelium were pooled and used as positive reference sera in enzyme-linked immunosorbent and immunofluorescence assays as described below. Sera pooled from another group of animals immunized in the same way with air-dried mycelium from *Trichoderma viride* (a common saprophyte on seeds) served as a negative reference serum.

Enzyme-linked Immunosorbent Assays (ELISAs)

Enzyme-linked immunosorbent assays were performed as described by Voller and others (1976) with the following modifications. Wells of 96 well, flat-bottomed polystyrene microtiter plates (no. 3590 Serocluster, Costar, Cambridge, MA) were coated with 50 µL/well of fungal soluble antigens adjusted to a protein concentration of 10µg/mL in distilled water. The plates were dried overnight at 37°C, then well sites not coated with antigen were blocked by adding 200 µL of 1% bovine serum albumin (Fraction V) in PBS (pH 7.4) to each well and incubating for 2 hr at room temperature. All other aspects of the assay were conducted as described by Voller and others (1976) using 50 µL volumes/well of hybridoma culture fluids or dilutions of ascites fluids in the first antibody layer and the same volumes of optimal dilutions of enzyme-labelled second antibody. Enzyme-labelled second antibodies employed were anti-mouse $IgF(ab')_2$-alkaline phosphatase conjugate (Helix Biotech, Vancouver, B.C.) or anti-mouse IgG (H + L)-peroxidase conjugate (HyClone Labs., Logan, UT) which were used to detect antibodies of all classes. Alkaline phosphatase-labelled chain-specific second antibodies, anti-mouse IgM (µ-chain) and anti-mouse IgG (γ-chain) were used to detect antibodies of the IgM and IgG classes, respectively. All second antibodies were affinity-purified and no binding to *Sirococcus* or other fungal antigens was observed in the absence of specific antibody. In assays where alkaline phosphatase-labelled second antibodies were employed 4-nitrophenyl phosphate (Boehringer-Mannheim, Dorval,Que.), 1 mg/mL in diethanolamine buffer pH 9.8 (0.97% v/v diethanolamine containing 0.02% NaN_3 and 0.1 mg/mL $MgCl_2.6\ H_2O$) was used as the substrate. The enzymatic reaction was allowed to proceed for 45 min in the dark at room temperature then stopped by adding 50 µL/well of 3 M NaOH and A_{405} was determined for each well with a MicroELISA Minireader (Series MR 590, Dynatech, Alexandria, VA). In assays where peroxidase conjugate was used the substrate solution consisted of o-phenylenediamine (Fisher, Vancouver, B.C.), 0.4 mg/mL and 3% H_2O_2, 4 µL/mL (v/v) in citrate buffer (pH 5.0). The microplates were incubated in darkness for 15 min at room temperature. The enzymatic reaction was stopped by adding 50 µL of 2.5 M H_2SO_4 to all wells and A_{490} was determined for each well.

Indirect Immunofluorescence Assays (IFA)

Unit layers of mycelium were grown on acid washed sterile 18 mm^2 glass coverslips (mounted on autoclaved filter paper disks moistened with MB in covered Petri dishes) by inoculating them with 1 drop of medium from sporulated cultures. When hyphae were visible the coverslips were removed individually to 60 mm glass Petri dishes and washed with 5 mL PBS containing 10% fetal calf serum (FCS) for 15 min at room temperature. The PBS/FCS was suctioned off and replaced with 100 µL of undiluted culture fluids and incubated in a moist chamber at room temperature for 1 hr. The coverslips were washed with 10 mL PBS/FCS and suctioned

dry. One hundred µL of fluorescein (FITC)-conjugated second antibody (anti-mouse IgG or anti-mouse IgM chain-specific sera, Kirkegaard and Perry, Gaithersburg, MD diluted to 1/20 in PBS/FCS and centrifuged for 5 min at 12000 x g) were added to each coverslip and incubated for 1 hr at room temperature. The coverslips were washed as before and inverted onto glass slides with 1 drop of mounting medium (90% glycerol in PBS, with 1 mg/mL o-phenylenediamine). The slides were examined with a Zeiss Photoscope II equipped with a 100 illuminator (fitted with an HBO 50 W high pressure Hg source), epifluorescence condenser III RS, 390-440 nm excitation and 475 nm barrier filters, 10x and 40x Neofluar objectives and 10x Kpl-w eyepieces.

Derivation of Hybridomas

Media and supplements.--RPMI-1640 medium, glutamine (200 mM), gentamycin (50 mg/mL), 4-(2-hydroxyethyl)-1-piperazine ethanesulfonic acid (HEPES, 1 M) were obtained as sterile solutions from Gibco Canada Ltd., Burlington, Ont. Sodium pyruvate, 2-mercaptoethanol, hypoxanthine, aminopterin, thymidine, dimethylsulfoxide (DMSO) and 2, 6, 10, 14-tetramethylpentadecane (Pristane) were obtained from Sigma, St. Louis, MO. Polyethylene glycol (Serva 1550) was from Terochem Labs., Edmonton, Alta. Fetal calf serum (FCS), preselected for its ability to support optimal growth of the myeloma cells used in fusion (see below) was supplied by Animal Health Labs., Islington, Ont. FCS was heat-activated (56°C for 30 min) prior to use as a medium supplement.

Myeloma cells.--SP2/0-Ag14, a nonsynthesizing myeloma cell line of BALB/c mouse origin (Shulman and others 1978) was obtained from Dr. T.W. Pearson (Department of Biochemistry and Microbiology, University of Victoria, B.C.). Prior to their use in cell fusion, the cells were grown for several passages in log phase in growth medium consisting of RPMI-1640 supplemented with 10% FCS, 0.5 mg/mL gentamycin, 2 mM glutamine, 1 mM Na puruvate and 0.1 mM 2-mercaptoethanol.

Cell Fusions.--Media, supplements and solutions used in cell fusion were prepared as described by Pearson and others (1980). All procedures were carried out under aseptic conditions. BALB/c mice that had been hyperimmunized with dried mycelium and rechallenged by intravenous injection of soluble antigens from *S. strobilinus* were used as spleen cell donors. Spleens were dispersed into single cell suspensions in fusion medium consisting of RPMI-1640 medium supplemented with 20% FCS, 0.5 mg/mL gentamycin, 2 mM glutamine, 1 mM Na pyruvate, 0.1 mM 2-mercaptoethanol and 10 mM HEPES, washed twice by centrifugation at 500 x g for 10 min at 4°C and adjusted to 1×10^7 or 2×10^7 cells/mL in the same medium. Log phase SP2/0 cells were washed once by centrifugation and adjusted to 1×10^6 or 2×10^6 cells/mL in fusion medium. Immune spleen cells and myeloma cells were mixed at a ratio of 10:1 and fused in the presence of polyethylene glycol as described by Pearson and others (1980). The fused cells were immediately dispensed in 50 µL aliquots into wells of 96 well microculture plates (no. 25860, Corning, Palo Alto, CA), supplemented with 160 µL/well of fusion medium containing 6.25×10^4 normal BALB/c mouse thymocytes as feeder cells and cultured for 18 hr at 37°C in 10% CO_2 in air. At the end of this period, the medium was removed and replaced with 150 µL/well of selective medium (HAT medium, consisting of fusion medium with 13 µg/mL hypoxanthine, 0.2 µg/mL aminopterin and 3.9 µg/mL thymidine). The microplates were returned to the incubator and fresh HAT medium added to the wells on days 7 and 14 after cell fusion. During this period the microplate wells were checked frequently for cell growth. When colonies were visible, culture fluid from each well was tested in ELISA for specific antibody. The contents of wells producing *Sirococcus*-specific antibody were removed to 1 mL of HT medium (fusion medium supplemented with 13 µg/mL hypoxanthine and 3.9 µg/mL thymidine) containing 1×10^6 thymocytes/mL in 24 well culture plates (no. 3524, Costar). After cell expansion, antibody specificity was checked by testing the medium in each well in ELISA using soluble antigens from either *Sirococcus* or *Trichoderma*. Hybridoma cells from wells that were positive for *Sirococcus* but negative for *Trichoderma* were cloned by limiting dilution as described below.

Limiting Dilution Cloning of Hybridomas

Hybridomas were cloned twice by diluting cells to 80, 20 and 10 cells/mL in cloning medium consisting of HT medium (first cloning) or fusion medium (second cloning) with 1×10^6 thymocytes/mL. For each dilution, 0.1 mL/well was pipetted into 12 wells of microculture plates to give cell densities of 8, 2, and 1 cell/well, respectively. After incubation at 37°C in 10% CO_2 in air for 7-14 days, wells were screened for specific antibody production and selected clones were expanded and cryopreserved or injected into mice for ascites production as described below.

Freezing and Thawing of Hybridomas

Hybridoma cells obtained from log phase culture were adjusted to 2×10^6 to 1×10^7 cells/mL in 90% FCS/10% glycerol and cryo-preserved in 1 ml aliquots in liquid nitrogen. To re-establish hybridomas in culture, the cells were thawed rapidly in a 37°C water bath and immediately centrifuged through 10 mL of warmed fusion medium. Cells were resuspended in 3-5 mL of the same medium in 25 cm^2 culture flasks which were gassed with 5% CO_2 in air, sealed and incubated as described above.

Production of Ascites

For production of ascites tumors, 1-2 x 10^7 hybridoma cells in a volume of 0.2 mL were injected i.p. into BALB/c mice primed (by i.p. injection) 10 days previously with 0.5 mL of Pristane. Ten to 14 days later the animals were killed and the ascites fluids removed aseptically from the peritoneal cavity. Cells were pelleted by centrifugation at 500 x g for 10 min at 4°C and cryopreserved as described above. The supernatant was filtered through cotton wool then stored in 0.2 mL aliquots at -20°C.

RESULTS

Derivation of Hybridoma Cell Lines Producing Monoclonal Antibodies Directed to *Sirococcus strobilinus*.

Two independent cell fusions (SDM1 and SDM2) were conducted using different spleen cell (SPLC) and myeloma cell (SP2/0) cell densities as described in Methods. Macroscopic colonies were visible in microculture plate wells within 7 days and culture fluid from each well was tested for specific antibody by ELISA 11 days after fusion. In fusion SDM1 in which SPLC and myeloma cells were mixed at a ratio of 1 x 10^7:1 x 10^6, 31 wells out of 480 contained antibody-producing hybidomas. The second fusion (SDM2) conducted at higher SPLC:myeloma cell densities (2 x 10^7:2 x 10^6) resulted in 7/480 wells which were positive for antibody production.

Cells producing specific antibody were expanded in 24 well culture plates and five days later, culture medium from each well was tested for specific antibody in ELISA using soluble antigens from *S. strobilinus* or *Trichoderma viride* or extraction buffer to coat ELISA plate wells. In 11 of the wells tested, antibodies in the culture fluids bound only to *Sirococcus* antigens, while in nine of the wells, antibodies which bound to both *Sirococcus* and *Trichoderma* antigens as well as extraction buffer-coated wells, were present. Those cells producing antibodies which recognized only *Sirococcus* soluble antigens were cloned twice by limiting dilution. After each cloning, hybridoma cells were tested for specific antibody production by ELISA. As a result, 30 stable cloned hybridoma cell lines producing *Sirococcus*-specific monoclonal antibodies (McAbs) were established. These cell lines are clones originating from five different (parental) wells in the initial fusion plates (indicated by the numbers 475, 441, 434, 171 and 392 in table 1). For each line, cells were cryopreserved in liquid nitrogen and McAb isolated from culture or ascites fluids. Twelve of the hybridoma lines (of the series 441 and 171) produce McAbs of the IgM class, while 18 (series 434, 475 and 392) hybridoma lines produce IgG McAbs as determined in ELISA using chain-specific second antibodies.

Analysis of Monoclonal Antibody Specificity

Antigen recognition in other Sirococcus strobilinus isolates.--As the primary goal of producing *S. strobilinus*-specific McAbs was to develop a diagnostic reagent for detecting this

Table 1.--Reactivity of *Sirococcus*-directed monoclonal antibodies with soluble antigens from other *Sirococcus strobilinus* isolates

		A_{490} nm/Hybridoma[1]				
Sirococcus isolate	Host[2]	SDM 1/475.6a.9	SDM 1/441.4.4	SDM 1/434.15.21	SDM 1.171.27.13	SDM 2/392.2.4
2456	ES	2.00	2.00	2.00	2.00	2.00
8652	SS	1.33	0.39	0.35	2.00	1.25
2231	SS	2.00	0.74	2.00	1.67	0.27
8615	WS	1.41	1.96	0.49	2.00	1.92
4321	IS	1.55	2.00	0.39	2.00	1.79
RR	LP	1.75	1.85	0.73	2.00	0.79
2311	LP	2.00	1.11	0.71	2.00	0.42
4248	LP	1.46	1.19	1.44	2.00	1.15
2247	WH	0.46	0.00	0.00	1.89	0.08

[1] McAbs produced by SDM hybridoma cell lines were tested in ELISA using soluble antigens (at 10 μg/mL) prepared from the isolate used in their derivation (2456) and eight other *S. strobilinus* isolates, to coat ELISA plate wells. A positive A_{490} nm value indicates reactivity of the McAb with its antigen in the soluble antigen mixture.

[2] ES = Engelmann spruce, SS = Sitka spruce, WS = white spruce, IS = Interior spruce, LP = Lodgepole pine, WH = western hemlock.

pathogen in seeds, it was important to ensure that the McAbs were not isolate-specific. Therefore, culture fluids obtained from each hybridoma line were tested in ELISA using soluble antigens prepared from nine different isolates of S. strobilinus from several host species and tissues. The results of assays done on representative clones of each parental cell line are shown in table 1. The results obtained with McAbs from other clones within each parental line were similar. Thus, the McAbs produced by the hybridomas collectively recognized antigen(s) present in all the Sirococcus isolates tested. However, differential patterns of reactivity were observed with different Sirococcus isolates and McAbs originating from different parental lines.

Specificity of monoclonal antibodies for Sirococcus strobilinus.--As Sirococcus is frequently associated with nonpathogenic fungi in or on seeds, it was necessary to ensure that the McAbs did not recognize antigens common to Sirococcus and other saprobes. Therefore, the McAbs were tested in ELISAs using soluble antigens prepared from Sirococcus or soluble antigens from seven different genera of commensal fungi all isolated from the same infested seedlot (2456) to coat microtiter plate wells. The results (table 2) showed that all McAbs were specific for S. strobilinus antigens and did not crossreact with antigens from commonly found saprophytic fungi. Although all the McAbs produced by the hybridoma lines were tested for specificity, only data from representative clones of each parental line are shown.

Monoclonal antibodies from representative hybridoma lines were also tested in indirect surface immunofluorescence assays (IFA) against mycelium from Sirococcus and the same commensal isolates. Although some of the McAbs recognized antigens exposed on the surface of Sirococcus mycelium (see below), none of the McAbs bound to mycelium of other fungal genera.

Morphological Distribution of Antigens Recognized by Sirococcus-Directed Monoclonal Antibodies.

Recognition of secreted antigens.--Monoclonals from representative hybridoma lines were tested in ELISAs in which ethanol-precipitated antigens from fungal culture medium (secreted antigens) were used to coat microplate wells. Several clones representing different parental hybridoma lines were tested. The data in table 3 show that two of the hybridoma lines (SDM 1/441.8.2 and SDM 1/171.27.13) produced McAbs which recognize antigen(s) that are also secreted into the culture medium by Sirococcus. No binding to

Table 2.--Reactivity of Sirococcus-directed monoclonal antibodies with soluble antigens from Sirococcus and other fungi

Fungus Genus[2]	A_{490} nm/Hybridoma[1] SDM 1/475.6a.5	SDM 1/441.4.4	SDM 1/434.15.21	SDM 1.171.27.22	SDM 2/392.2.4
Sirococcus	1.91	1.06	1.23	0.71	0.87
Trichoderma	0.05	0.14	0.04	0.10	0.03
Alternaria	0.04	0.05	0.03	0.04	0.03
Paecilomyces	0.05	0.05	0.05	0.11	0.04
Sclerophoma	0.03	0.03	0.02	0.03	0.02
Penicillium	0.04	0.04	0.04	0.07	0.03
Rhizopus	0.02	0.03	0.01	0.01	0.01
Mucor	0.02	0.02	0.02	0.02	0.01
Extraction Buffer	0.02	ND	0.01	0.02	0.04

[1] McAbs antibodies produced by SDM hybridomas were tested in ELISA using soluble antigens from S. strobilinus or from seven different fungal genera to coat microplate wells.

[2] Soluble antigens prepared from S. strobilinus and seven other fungal isolates from seedlot 2456 were coated onto ELISA microplate wells at a concentration of 10 µg protein/mL. Extraction buffer (see Methods) coated at 1/10 dilution served as a control.

secreted antigens of *Penicillium* was observed with any of the McAbs tested.

Recognition of surface antigens.--Monoclonals from representative hybridoma lines were tested in IFA for their ability to recognize antigens exposed on the surface of mycelium grown on MB. Pale yellow autofluorescence in mycelial preparations caused a background which interfered with interpretation of low levels of FITC (green) fluorescence due to specific antigen-antibody interactions. Therefore, the McAbs were tested several times in separate assays. Although the majority of the McAbs did not bind to the surface of *Sirococcus*, some McAbs produced two distinct patterns of fluorescence. Some McAbs produced bright patches of fluorescence at what resembled thin areas of the cell wall often near the hyphal tip or at broken ends of the hyphae ("patchy surface" fluorescence). Other McAbs produced bright punctuate fluorescence at structures resembling holes in the cell wall and on fibrillar material surrounding the hyphae ("patchy surface + fibrils"). These observations are summarized in table 4.

Table 3.--Reactivity of *Sirococcus*-directed monoclonal antibodies with fungal secreted antigens

SDM Hybridoma	A_{490} nm/Antigen[1] Sirococcus	Penicillium
1/434.15.21	0.08	0.05
1/171.27.13	2.00	0.07
1/441.8.20	0.68	0.05
1/475.6a.10	0.02	0.01
2/392.10.20	0.10	0.04

[1] Fungal secreted antigens were prepared by ethanol-precipitation of spent culture medium (see Methods).

DISCUSSION

This paper has described the derivation by cell fusion techniques of monoclonal antibodies (McAbs) which recognize antigens of the fungus, *S. strobilinus*. This approach was necessary as preliminary investigations (unpublished) with polyclonal antisera raised in rabbits and mice by immunizing them with *Sirococcus* extracts revealed a considerable amount of cross-reactivity between *Sirococcus* and other nonrelated seed-associated fungi, presumably due to shared antigenic determinants. McAbs, which recognize a single site on an antigen molecule (Milstein 1980), may be selected for their ability to recognize unique antigenic sites in related organisms and therefore circumvent the problems of crossreactivity often observed with antisera. The *Sirococcus*-directed McAbs described herein did not recognize internal or surface antigens of nine different nonrelated fungi often associated with *Sirococcus* in seeds. Therefore, these McAbs are probably directed to unique antigens of *S. strobilinus* and will serve as useful diagnostic reagents for detecting this conifer pathogen in seeds or other tissues. These McAbs, as a group, also recognized antigens of eight other *S. strobilinus* isolates obtained from diverse host species and tissues. Therefore, the McAbs, although derived

Table 4.--Surface immunofluorescence patterns observed with *Sirococcus*-directed monoclonal antibodies

SDM Monoclonal Antibody	Fluorescence Distribution[1] Negative	Patchy Surface	Patchy Surface & Fibrils
1/441.4.2	● ●	● ●	
1/441.8.6	●		
1/441.8.18			●
1/171.21.16	● ●	●	
1/171.21.22		●	
1/434.15.9	● ●	●	
1/434.28.5	●		
1/475.6a.2	●		
1/475.6a.4		●	
2/392.5.31	●		● ●
2/392.2.4	● ●	●	
2/392.10.20		●	

[1] McAbs from representative SDM hybridoma cell lines were tested for surface binding to unit layers of *Sirococcus strobilinus* mycelium. Bound McAbs were detected with a mixture of FITC-conjugated goat anti-mouse IgM and goat anti-mouse IgG second antibodies at 1/20 dilutions. Each dot represents the results of one assay conducted with the monoclonal antibody.

using a single isolate, were not isolate-specific and can be used generally to detect this fungus. The observed differential patterns of reactivity of the monoclonals with other Sirococcus isolates suggest that they recognize more than one antigen and/or there is differential expression of these antigens in Sirococcus obtained from varied sources. Although all McAbs tested recognized antigens in isolates from spruce and pine hosts, only five hybridoma clones produced McAbs which recognized antigen(s) of Sirococcus isolated from western hemlock.

A preliminary characterization of the morphologic distribution of the antigens recognized by these McAbs indicated that some antigens may be exposed on the surface of the fungus and/or may be secreted into culture fluids. As mice were immunized with whole mycelium and therefore were exposed to the whole antigenic repertoire of the fungus, antibodies directed to both internal and surface antigens would have been generated. However, as antibodies produced by the hybridomas were selected in ELISA using only soluble antigens, a predominance of antibodies directed to internal components would be expected. Indeed, this was the case, as the majority of the McAbs did not react with the mycelial surface in IFA. However, several of the monoclonals exhibited a patchy distribution of surface fluorescence in these assays. Whether this represents reactivity of the McAbs with cell wall antigen(s) (that were also present in the soluble antigen preparation used in ELISA) or accessibility of the antibodies to an internal component through a lesion or thinning of the cell wall, is speculative. The variability in IFA fluorescence patterns may also reflect the age and physiologic state of the mycelial material used in the assays. Two monoclonals (SDM 1.172.27.13 and SDM 1/441.8.20) reacted in ELISA with Sirococcus secreted antigens. Another clone (SDM 1/441.8.18) produced antibody which reacted in IFA with both the mycelial surface and associated fibrillar material. Perhaps the antigens recognized by these McAbs may be enzymes or secondary metabolites that are transported to the exterior of the fungus.

The specificity of the Sirococcus-directed McAbs described here will allow their use as diagnostic probes for this pathogen in seeds and other plant tissues. Sensitive immunologic assays employing these McAbs are currently being developed with the objective of establishing a simple, rapid and accurate method for screening seedlots destined for use in forest nurseries or for export.

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IMPACT OF INSECTS ON SEED PRODUCTION IN A DOUGLAS-FIR SEED ORCHARD

Scott A. Dombrosky and Timothy D. Schowalter

ABSTRACT: The impact of various factors on seed production in a Douglas-fir (*Pseudotsuga menziesii*) seed orchard in western Oregon was examined by monitoring the fate of seeds in 30 cones, stratified into three crown levels, on each of 10 trees during the 1984 growing season. Cones were examined monthly between April and September for mortality or evidence of insect damage. In September a sample of mature cones was collected and completely dissected. Each seed was examined for extractability, insect damage, or unexplained abortion. These data were used to measure the relative impacts of various cone and seed mortality agents, and to develop an inventory monitoring system for management of Douglas-fir seed production. The results of this study indicate that, in addition to the recognized importance of insects to seed loss at cone maturity, insects also cause seed production losses through early conelet abortion in Douglas-fir.

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SELECTIVELY HARVESTING CONES WITH A FANDRICH AERIAL RAKE

Helmut Fandrich

ABSTRACT: Selecting the trees to be harvested from the air allows the forester to specify harvesting areas, elevations, type of trees and even specific trees. Aerially picking dominant trees at selected intervals with a Fandrich rake gives the forester the opportunity not only to freely specify the best trees from a broad genetic base, but also to rapidly collect large volumes during heavy crop years when the yields are higher and the costs are lower. The rate of picking can be estimated if one knows the quantity of cones near the top of the trees since the pilot will rake approximately one tree per minute.

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ASSESSING INDIVIDUAL SPECIES' IMPACT ON SEED YIELD AND COMMUNITY INTERACTIONS AMONG CONE AND SEED INSECTS

Nancy Rappaport

ABSTRACT: Methods are described for assessing individual species' impact on seed yield and community interactions among cone and seed insects. The procedure involves sequentially bagging cones to exclude all possible combinations of species. These exclusions may be viewed as a series of simulated pesticide applications. Thus, in our study, we excluded each of the three major pests of Douglas-fir cones singly and in combination with the other pest species. This was possible because there was a degree of nonoverlap in the oviposition phenologies of the principal pest species. Cones were left bagged during the oviposition periods of each species, then were exposed to allow oviposition by the other species. This permits assessment of impact by individual species and also yields information about potential associative and competitive interactions among the species. Such interactions may have important consequences for our pest management strategies, particularly if our treatments remove only certain of the pest species.

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USE OF SYSTEMIC INSECTICIDES TO PROTECT INDIVIDUAL TREES FROM WESTERN SPRUCE BUDWORM

Richard C. Reardon

ABSTRACT: Implantation and injection methods are described for protection of individual trees from western spruce budworm. Implantation is with Medicaps which contain a dry chemical; injection is with Mauget Systemic Injector Units which contain a liquid formulation. Impact of consecutive yearly applications in reducing western spruce budworm populations and in response of trees to wounding is described. The advantages and disadvantages of each method are compared.

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YIELD AND VIABILITY OF NORTHERN LODGEPOLE PINE SEED

Allen Richmond, John Alden, Thomas Malone, and Robert Van Veldhuizen

ABSTRACT: Lodgepole pine (*Pinus contorta* Dougl. ex Loud.) is the most widely planted conifer in boreal forests. Demand for seed from northern populations has accelerated cutting of trees for cone harvest. Populations from central Yukon are discontinuous and may not produce enough seed to meet demands unless utilization of cone crops is improved. At the present time, only cones from the 2- to 5-year age class are usually recommended for commercial collection.

Serotinous cones were found to contain viable seed to 55 years of age. Seed age had no effect on seed vigor as measured by rate of real (viable seed) germination. Seed recovery was not affected by age of cones. Seed viability declined with age, but still maintained relatively high germination rates to 20 years of age. The seed not collected in the 6- to 20-year age classes represents a wasted seed resource. Portions of this resource should be utilized as its viability and vigor are only slightly lower than seed from 2- to 5-year-old cones.

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DEFOLIATION AND DOUGLAS-FIR CONE AND SEED LOSSES CAUSED BY BUDWORM IN THE NORTHERN U.S. ROCKY MOUNTAINS

Raymond C. Shearer

ABSTRACT: In September 1979, counts of ovulate buds on 25 randomly selected branchlets on each of 22 Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) trees at 20 locations in the Northern U.S. Rockies predicted a good cone crop for 1980 throughout the study area. However, potential cone crop was nearly eliminated in areas of moderate to high defoliation by western spruce budworm (*Choristoneura occidentalis* Freeman), especially in Montana east of the Continental Divide and in nearby east-central Idaho. Few cones matured in stands with a 1980 defoliation-rating index greater than 40 percent. Stands with low to moderate defoliation-rating indexes (from 30 to 40 percent) had from 30 to 90 percent of the potential cones killed by budworm larvae. The remaining stands had low defoliation rating indexes (from 2 to 21 percent) and low cone mortality caused by budworm larvae (from 2 to 25 percent of the cone potential). Most of the mortality occurred during the early stages of cone development (92 percent were killed by budworm larvae in the bud or erect conelet stage). These losses accounted for about 80 percent of all seed mortality caused by budworm.

The remaining 20 percent of budworm-caused seed mortality occurred in mature cones. Budworm larvae reduced the number of viable seed in mature cones by 1 to 32 percent, depending on location. Seed loss in live cones increased in areas of greater defoliation. Other insects causing seed losses in mature cones were a cone moth (probably *Barbara colfaxiana* [Kearfott]), a cone worm (probably *Dioryctria* sp.), a scale midge (probably *Contarinia washingtonensis* Johnson), a seed chalcid (probably *Megastigmus spermotrophus* Wachtl), and a seedbug (probably *Leptoglossus occidentalis* Heidemann).

Forest managers should not depend on Douglas-fir cones to provide seed for artificial or natural regeneration when the stand-defoliation index is greater than 30 percent, even in years of potentially heavy cone production. Budworm larvae also decrease seed production in stands with defoliation under 30 percent. To protect Douglas-fir cone crops, insecticide should be applied when the cone and pollen buds open.

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REDUCING DOUGLAS-FIR SEED AND CONE DAMAGE

Lawrence E. Stipe

During 1979 and 1980, single, double, and triple ground applications of acephate and carbaryl were used to improve Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) seed and cone production in areas of moderate to heavy western spruce budworm (*Choristoneura occidentalis* Freeman) populations. Ten single-tree replications were used for all treatments. Cone-bearing Douglas-fir trees 9 to 18 m (30 to 60 ft) tall were selected by examining cone buds, then randomly assigned one of the three treatments. Mixing and application rates were according to label instructions: acephate--400 g (300 g Al) in 500 L water (2/3 lb. [1/2 lb. Al] in 100 gal. water); and carbaryl--2.5 L (1.2 kg Al) in 500 L water (2 qt. [1 lb. Al] in 100 gal. water).

Each tree was sprayed beyond the point of runoff with a hydraulic pumper and handgun operated at 28 kg/cm^2 (400 lb/in^2). The single application, timed to coincide with peak second instar spring dispersal, was on May 21, 1979, when cone buds had expanded to 2.54 cm (1 in) long and were still erect. Postspray densities of fourth instars for acephate, carbaryl, and control were 3.6, 1.3, and 21.2 larvae per 100 shoots, respectively; defoliations after pupation were 10.8, 2.2, and 73.0 percent, respectively. Of the potential 68 seeds per cone, the single application provided seed production per cone of 0.5 seed for acephate, 1.0 seed for carbaryl, and no seeds for control. These less-than-expected results were primarily because budworm feeding had damaged over 30 percent of the cones before treatment and because subsequent cone damage by budworm and other seed-and-cone species had caused additional damage before cone harvest on August 23. To reduce prespray infestation losses and provide longer protection, double and triple applications were tested the next year. The first applications were on May 8 and 9, 1980, coinciding with the beginning of larval dispersal, which peaked on May 24. This earlier timing reduced prespray cone damage to less than 14 percent. The second applications were on May 27 and 28. The last of the triple application was on June 16. Postspray, mature budworm larvae per 100 shoots for acephate, carbaryl, and control were 0.9, 0.6, and 16.3 for double application and 0.3, 0, and 16.3 for triple application; defoliation was 4.8, 0.9, and 77.5 percent for single application, 1.1, 0.6, and 77.5 percent for double application, and 1.3, 0.6, and 77.5 percent for triple application. Mature cones were collected on August 18. Total seed yield for acephate, carbaryl, and control was 34.2, 41.4, and 22.5. Total seed yield for all spray treatments was significantly different from the control, but no significant differences were found between acephate and carbaryl or between double or triple applications. Seed condition (sound, hollow, and insect-damaged) and germination differences were small, variable, and not related to treatment. Where seed yields are important and budworm populations are moderate to heavy, a double application of either acephate or carbaryl is recommended. Time the first application when budworm larvae first begin spring dispersal, and follow with a second in about 14 days.

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SYMPOSIUM SUMMARY: CONIFER TREE SEED IN THE INLAND MOUNTAIN WEST

Stanley L. Krugman

In spite of the recent advances in tree propagation, such as tissue culture and mass rooting, seeds will remain the major source of planting material for many years to come. Each year we are dealing with more tree species from more areas. Each year we are working with a larger number and variety of seed lots as we attempt to better match seed source to site. As the genetics and tree improvement programs expand there is a continuous need for additional information including time of flowering, and improved methods of collecting, processing, storing, and germinating seeds.

Basically such information is needed to improve efficiency and to reduce field planting costs. Speakers throughout this meeting have addressed these issues from a number of different points of view. We have been fortunate to have researchers as well as regeneration specialists share their experiences with us. Predicting and stimulating seed production remains a major issue in western forestry. A further understanding of flowering biology and development is essential if a rational program is to be initiated. The review of cone and seed biology and development by John N. Owens demonstrated that there are a series of critical stages in cone and seed development. We need to have an understanding of them for our individual species under our local environmental conditions if we are to obtain maximum yield or at least reduce certain types of losses. Closely related is the use of hormones to stimulate flowering in some of our western species. Stephen D. Ross reviewed the current experience with hormones, their value, and limitations. Although the system is not perfect, for selected species and purposes we now have a valuable tool. Reports by Glenn L. Jacobsen, Allen S. Rowley, and Raymond C. Shearer pointed out that many conditions influence cone production and seed yield and our understanding of environmental influences is still very primitive. Interesting papers by Katherine A. Yakimchuk, R. J. Hoff, Carole L. Leadem, and A. K. Hellum provide new data on seed germination and methods for increasing germination. These papers and several others, however, demonstrated we are not consistent in defining germination. As noted by Katherine A. Yakimchuk, we need to consider both radicle elongation and seedling development. This is an important element since older seeds and immature seeds, as well as damaged seeds, when germinated may have radicle elongation but seedling development is abnormal and the resulting seedlings will perish in the nursery bed.

Biotechnology that offers unique opportunities in tree improvement may soon play a major role in reducing seedborne diseases. The research by Leslie Ann Mitchell suggests that the further development of appropriate monoclonal antibodies techniques will be a valuable tool in recognizing seedborne fungal pathogens. More traditional and nontraditional approaches to disease and insect protection were discussed by Michael I. Haverty, Patrick J. Shea, William F. Johns, and Richard C. Reardon. Although the methods are promising, most such techniques can only be used in high-value areas such as seed orchards or superior seed stands. As we increase our seed crops annually through manipulations we can expect an increase in disease and insect problems; improved protection techniques are badly needed.

A major value of this meeting, in addition to the sharing of current information and experiences, is that it brought the researchers and practitioners together. For the nurserymen and nurserywomen I would suggest that some of the problems raised by your papers and questions have already been answered by earlier research. It would appear to me that we still have an information gap. For the scientists in the audience I would like to once again state that your job does not end with the publication of a scientific paper but must include at least an attempt to translate the science into useful and, if possible, practical methods for the field user. To encourage such activities we need to in the future, as we did here, bring the field user groups and the scientists together in common meetings. I believe we all found the meeting of use and I look forward to the published proceedings.

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Includes six reviews and 34 papers presented in four technical sessions: cone and seed biology; cone prediction, collection, and processing; seed orchard and seed production area management; and effects of vertebrates, insects, and diseases on seed production. Current information is presented on conifer tree cones and seeds native to the Inland Mountain West (east slopes of the coastal ranges to the plains of the United States and Canada).

KEYWORDS: conifers, cone and seed biology, seed orchards, seed production area, cone and seed damage

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